# EVOLUTION OF PREDATION-RELATED CHARACTERS IN NEOGENE ATLANTIC COASTAL PLAIN CORBULIDS AND LUCINIDS

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A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
Of the Requirement for the Degree of
Master of Science

Department of Earth Sciences

University of North Carolina at Wilmington

2003

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This thesis has been prepared in a style and format

Consistent with the journal Palaios.

TABLE OF CONTENTS

ABSTRACT

The hypothesis of escalation proposes that biologic hazards, such as predation, have increased through the Phanerozoic and that these hazards are important agents of selection. Traits that give organisms an advantage over their enemies (predators, competitors, and dangerous prey) should become better expressed with time. The naticid predator-prey system is ideal for testing the hypothesis of escalation, because the characteristic predatory drill holes made by naticid gastropods in their hard-shelled prey produce a fossil record of predator-prey interaction. Three species from the bivalve families Corbulidae and Lucinidae from the US Atlantic Coastal Plain ranging in age from Miocene to Pleistocene were examined in this study. Anti-predatory related morphologic characters (valve thickness, internal volume, and cost-benefit ratio) were traced through the time interval studied. Valve thickness and cost-benefit ratio were hypothesized to increase with time. Internal volume was hypothesized to decrease with time. Three of nine predicted trends in anti-predatory morphology were confirmed. Valve thickness increased in *Caryocorbula conradi*. Cost-benefit ratio increased in *C. conradi* and *Parvilucina crenulata*. The evolution of anti-predatory traits was not correlated with changes in drilling predation intensity nor prey effectiveness. The evolution of anti-predatory morphology by the corbulids and lucinids may have been outpaced by the evolution of the naticid predators. Determining causes in the evolution of shell morphology is complicated, but the driving force of evolution is likely attributable to selection produced by predators, primary productivity, and abiotic factors.

ACKNOWLEDGMENTS

Many thanks go to my advisor, Tricia Kelley. Her guidance, patience, love for teaching, love for her science, and genuine concern for others has benefited me greatly. I am proud to call her my mentor. The support and instruction given by my committee members Richard Laws and James Dockal is greatly appreciated. I enjoyed our conversations in and out of the classroom.

I have gained much from the many hours spent talking with Greg Dietl about all manner of topics ranging from predation on clams to predation on Doritos. Thanks for introducing me to behavioral ecology. I value the times spent in the field with Greg and Heyward Key. Long live covert geology and the three Craigs!

The graduate students in the department of Earth Sciences have been a wonderful source of camaraderie and good times. Without their support and friendship, my stay in Wilmington would not have been nearly as enjoyable.

Most of all, many thanks to my family: Tom, Frieda, and Adam. Your multifaceted support throughout the years means so much to me. Thank you for the encouragement and love. And yes, eventually I will get a job.

A Stephen Jay Gould Grant-in-Aid from the Paleontological Society, graduate student research grants from the Geological Society of America and Southeastern Section of the Geological Society of America, and a Victor A. Zullo Memorial Scholarship and Earth Sciences Research Grant from the University of North Carolina at Wilmington supported this research.

# DEDICATION

This thesis is dedicated to the loving memory of my grandfathers, Warren Calvin Huntley and John Lewis McCrary.

LIST OF TABLES

LIST OF FIGURES

# INTRODUCTION

## Brief History of Evolutionary Theory

With the publication of the *Origin of Species* (Darwin, 1859) came an explanation of the history of life based upon methodological naturalism. Darwin proposed a mechanism designated natural selection that explained the diversity of life seen today. Natural selection can be summarized by three tenets:

1) There is an enormous amount of heritable variation within populations.
2) More offspring are born than can survive.
3) Individuals with any advantageous characteristics are more likely to survive and reproduce (Darwin, 1859).

Such a theory challenged the previously held views that species were immutable. Instead, species were seen as dynamic and stemming from common ancestors. Darwin realized that natural selection could preserve variation, but could not produce it. It would be another 60 years (the coming of the "Modern Synthesis") until the process of evolution by natural selection was very well understood (Eldredge and Gould, 1972). Darwin's view of evolution places great emphasis on the role of ecology. Interaction between predator and prey, competitors, and the physical environment is seen as the driving force modifying entire populations gradually into transformed descendants (sympatric evolution).

In 1972, views on the nature of evolution began to change. Eldredge and Gould (1972) authored a paper entitled "Punctuated Equilibria: An Alternative to Phyletic Gradualism." The authors suggested that paleontologists had been applying the

sympatric model of evolution, whereas they should have been applying the model currently held by biologists, allopatric speciation. Utilizing the sympatric model, most paleontologists expected to find well-documented gradual lineages within the fossil record. Eldredge and Gould stated that this gradual pattern, by and large, is not the pattern seen in the fossil record (an idea well exploited and misrepresented by creationists (Pennock, 2001)). Instead, they proposed, paleontologists should employ the allopatric model of speciation. Four statements can summarize the allopatric model of speciation:

1) New species arise by the splitting of lineages (speciation).
2) New species develop rapidly.
3) Small sub-population of ancestor gives rise to descendant species.
4) Descendant species originate in a small section of the ancestor species' geographic range.

With this model of speciation in mind, two predictions can be made about what should be seen in the fossil record:

1) Sharp morphologic breaks should occur in local sections, which would represent the migration of the descendant species into the geographic range of the ancestor species.
2) Many morphologic breaks in the fossil record are real, and are not due to an imperfect geologic record. The stasis seen in fossil morphology is real, and can be viewed as data.

The birth of punctuated equilibrium marked a major shift in thought in paleontology. Many workers reasoned that if speciation was indeed a geologically rapid process that occurred in isolated patches, then natural selection within established species was not as important as originally thought. Gould (1985) proposed that evolution actually occurred within a hierarchy of evolutionary processes, in which change produced at lower tiers could be counteracted by events in upper tiers. Processes occurring in ecological time

reside in the first tier. Interactions between predator and prey and between competitors are typical of the first tier. At the second tier lie such processes as speciation and species selection. In species selection, selection operates on the random process of speciation, favoring species with long durations or high speciation rates (Stanley, 1975). Mass extinctions define the third tier. Gould saw mass extinctions as random catastrophic events, the victims of which could not be predicted. According to Gould, any change accrued on an ecologic time scale (first tier) would be negated by species selection (second tier). As would be expected, mass extinctions (third tier) would negate any change produced at the first and second tiers. Trends produced by ecological interactions should not be present in the fossil record since they likely occur on time scales finer than those that can be resolved in the fossil record (Gould, 1990)

Some workers did not agree with the notion that ecology did not matter in evolution. Allmon (1994) argued that ecology could matter in a macroevolutionary context (evolution above the species level) in one of two situations. First, stabilizing selection may be the source of stasis, as opposed to intrinsic constraints of the organism. Second, ecologic processes may be important in the three-staged process of allopatric speciation:

1) Isolated population forms.
2) Isolated population persists.
3) Isolated population differentiates from ancestor.

Ecologic processes such as competition and predation may be important in determining the success of organisms at any of the stages of allopatric speciation. For instance, competition for living space with incumbent species may keep an isolated population from persisting. While these situations are possibilities, Allmon (1994) called for further research to test these ideas.

Vermeij proposed the hypothesis of escalation in his book entitled *Evolution and Escalation: an Ecological History of Life* (1987). Vermeij suggested that biological environments have become more hazardous throughout the Phanerozoic, and that organisms must either adapt to better contend with their enemies, migrate to areas that are less hazardous, or become extinct. Vermeij stressed the familiar idea that predation and competition produce selection, and this selection drives evolution. Traits that give organisms an advantage over their enemies should increase through time. Abiotic processes such as changes in climate and productivity would regulate trends produced by ecological interactions. Escalation is more likely to occur in environments with an abundance of resources such as nutrients and thermal energy. Morphologic trends of escalation need not be unidirectional, but could be reversed or cyclical as well.

## Previous Studies of the Naticid Predator-Prey System

One system that is particularly useful in testing the hypothesis of escalation is the naticid gastropod predator-prey system. This system is practical for paleontological study in that naticids leave a characteristic borehole in their molluscan prey, producing a fossil record of predator-prey interaction. The Naticidae are characterized as being infaunal predatory gastropods that feed by enveloping their prey within the mesopodium and drilling through the prey's shell wall. Drilling is accomplished through intermittent scraping actions of the radula and acidic secretions from the accessory boring organ. Feeding is achieved through the proboscis, which is inserted into the countersunk borehole (Carriker, 1981; Kabat, 1990). Site selectivity of borehole placement on the prey is an innate behavior, not learned, in the modern naticid *Natica gualtieriana* (Berg,

1976). These generalizations do, however, have some exceptions. *Natica gualteriana* hunts subaerially at low tide in the intertidal zone at Bantayan Island, Philippines (Savazzi and Reyment, 1989). *Neverita duplicatus* is also known to forage subaerially during low tide in the intertidal zone near Wilmington, North Carolina, US (personal observation). Some naticids are known to feed on bivalves without drilling. Turner (1955) reported *Neverita duplicatus* feeding on the gaping razor clam *Ensis directus* between the valves. Turner also suggested that the slime coating produced by the naticid might have anesthetizing effects. Ansell and Morton (1987) reported *Glossaulax didyma* would smother larger prey after an unsuccessful drilling attempt in laboratory experiments in Hong Kong (for summary of exceptions to characteristic naticid behavior see Kelley and Hansen, 2003).

Laboratory experiments based upon the optimal foraging model show that naticids are selective predators, in that they will select the prey item with the lowest Cost-benefit ratio within the size range that the predator can handle (Kitchell et al., 1981). Kitchell et al. (1981) concluded that the primary factor in determining the cost of drilling a prey item was the thickness of the shell (correlated with drilling time), and the primary factor in determining the benefit was the internal volume (correlated with biomass). Some workers feel that this model is oversimplified due to costs incurred by the predator dealing with prey that utilize active defenses such as fleeing or dangerous prey (Leighton, 2002). However, the model is likely useful with sluggish infaunal bivalves that rely on passive defenses such as thick or ornate valves.

Passive defenses may be reflected in shell morphology, such as shell thickness. Changes in this and other characters can make a prey item more or less appealing to a

selective predator. Kelley (1989) investigated the evolution of shell thickness and internal volume in a bed-by-bed study of five genera of middle Miocene Chesapeake Group bivalves over the course of three million years. *Corbula*, *Lucina*, and *Eucrassatella* (predicted by Cost-benefit analysis and confirmed by drilling frequency to be preferred; with the exception of *Corbula* which was not confirmed by drilling frequency perhaps due to the presence of conchiolin layers) experienced net increases in valve thickness of 8%, 157%, and 72%, respectively. As thickness increased in these bivalves, naticid drilling frequency decreased. The prey of naticids predicted by Cost-benefit analysis to not be preferred (but not confirmed by drilling frequencies), *Astarte* and *Anadara*, displayed mixed results. *Astarte* experienced an initial increase in valve thickness but displayed a sharp decrease in the final stratigraphic interval. This produced a net change in valve thickness of –33%. Drilling frequency in *Astarte* displayed an initial increase and subsequent decrease. *Anadara* experienced a net increase in thickness of 94%. As one would predict, drilling frequencies in *Anadara* decreased as well. With the exception of an increase in *Astarte*, evolution of internal volume was characterized by non-directional fluctuation. Kelley (1991) demonstrated that these predation-related characters evolved at higher rates than did characters unrelated to predation. Evolution of valve thickness also occurred at higher rates in preferred prey than in non-preferred prey.

Kelley and Hansen (1993, 2003) examined the naticid predator-prey system and its implications for the process of escalation at the faunal level. Kelley and Hansen (1993, 1996) proposed a model for escalation based upon the cyclic rise and decline of faunal drilling frequencies through time. Drilling frequencies were tallied for bivalves, gastropods, and combined molluscan fauna from twenty-four stratigraphic intervals

ranging in age from Late Cretaceous to Recent from the U.S. Gulf and Atlantic Coastal Plains (Fig. 1). Drilling frequencies were relatively low in the Cretaceous, waned across the Cretaceous-Tertiary boundary, rose sharply following the Cretaceous-Tertiary boundary, and remained high until the late Eocene. Drilling frequencies declined at the Eocene-Oligocene boundary, and rose during the Oligocene. Drilling frequencies stabilized through the Oligocene into the early Miocene. Drilling frequencies rose sharply during the middle Miocene (though prior to the middle Miocene extinction), decreased and stabilized during the Pliocene and Pleistocene, and rose again in the Recent (Kelley and Hansen, 1993 and 2003). This pattern was interpreted as being cycles of escalation bounded by mass extinctions related to drops in productivity resulting in the preferential extinction of highly escalated taxa (as highly escalated taxa require more resources than less escalated taxa). Drilling frequencies rose after mass extinctions due to the absence of highly escalated taxa. Drilling frequencies subsequently stabilized and declined as the prey evolved more defenses. However, Hansen et al. (1999) failed to support the idea of preferential extinction of morphologically escalated species, though the idea may be supported if physiological characters such as growth rates are considered (Dietl et al., 2002).

## Objectives

This study investigates the evolution of anti-predatory characters of Neogene bivalves from the North American middle Atlantic Coastal Plain. Following a methodology similar to that of Kelley (1989), changes in valve thickness and internal volume are examined in corbulid and lucinid bivalves from the middle Miocene through

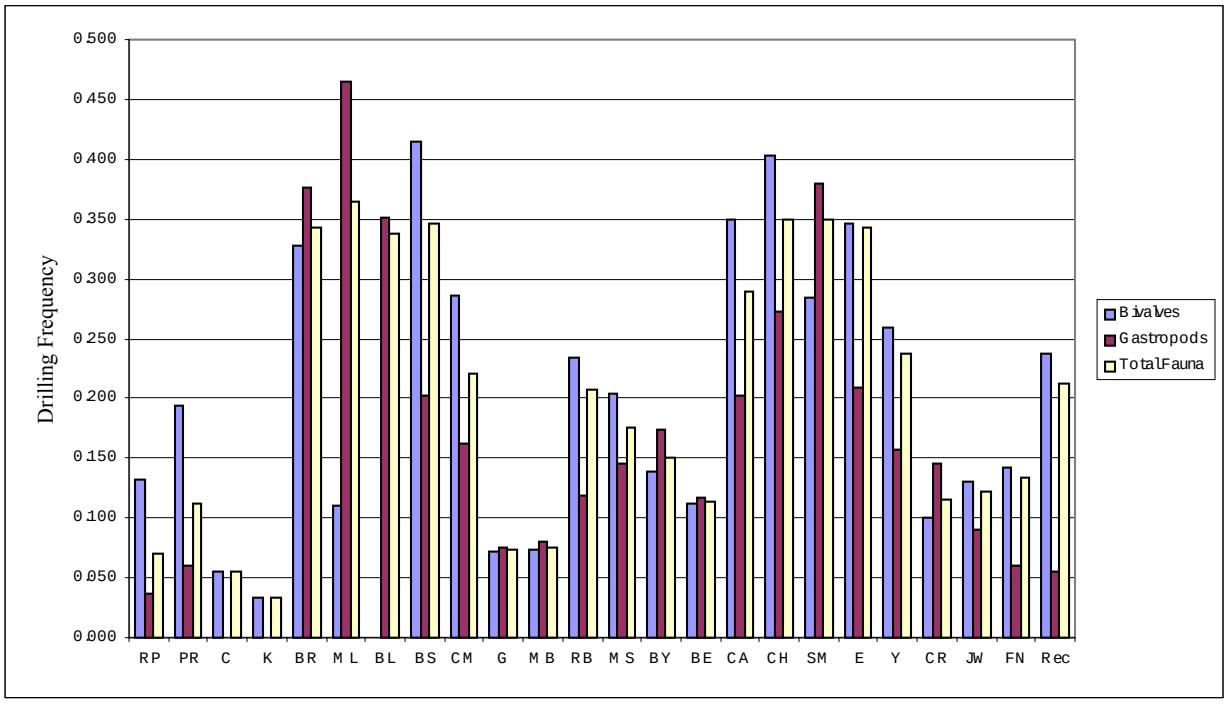



Figure 1. Drilling frequencies in bivalve, gastropod, and total molluscan fauna from the Late Cretaceous to the Recent (modified from Kelley and Hansen, 2003). Stratigraphic units: Cretaceous: RP, Ripley Fm.; PR, Providence Fm.; C, Corsicana Fm. Paleocene: K, Kincaid Fm.; BR, Brightseat Fm.; ML, Matthews Landing Mb. of Naheola Fm.; BL, Bells Landing Mb. of Tuscahoma Fm. Eocene: BS, Bashi Mb. of Hatchetigbee Fm.; CM, Cook Mountain, Upper Lisbon, and Piney Point Fms.; G, Gosport Fm.; MB, Moodys Branch Fm. Oligocene: RB, Red Bluff Fm.; MS, Mint Spring Fm.; BY, Byram Fm. Uppermost Oligocene/lower Miocene: BE, Belgrade Fm. Miocene: CA, Calvert Fm.; CH, Choptank Fm.; SM, St Marys Fm.; E, Eastover Fm. Pliocene: Y, Yorktown Fm; CR, Chowan River Fm. Pleistocene: JW, James City and Waccamaw Fms.; FN, Flanner Beach and Neuse Fms. Rec, Recent.

the Pleistocene. This study encompasses a greater amount of time than Kelley's (1989) study, though with less temporal resolution. This study will give more insight into whether first-tier processes can drive evolutionary trends seen in geologic time. Gould would argue that trends in adaptation such as an increase in valve thickness or decrease in internal volume in response to a drilling predator would be driven to their limit in a geologic instant and not found in the fossil record. The hypothesis of escalation might predict an increase in valve thickness and a decrease in internal volume. However, periods of escalation can be cyclical or temporarily reversed due to abiotic factors such as climate change or mass extinctions. Such may be the case if drilling frequencies of the genera in this study emulate those found at the faunal level.

## Hypotheses

It is my hypothesis that predators are an important agent of selection, in accordance with the hypothesis of escalation. Valve thickness relative to length will increase with time within species. Internal volume relative to length will decrease with time within species. Cost-benefit ratio relative to length will increase with time within species. An increase in valve thickness and/or a decrease in internal volume should result in lower drilling frequencies and higher prey effectiveness within a taxon. This predicted increase in expression of anti-predatory traits would support the hypothesis of escalation.

# MATERIALS AND METHODS

Specimens from the bivalve families Lucinidae and Corbulidae used in this study were taken from the collections of Kelley and Hansen, housed at the University of North Carolina at Wilmington and Western Washington University. The specimens are from bulk samples collected by Kelley, Hansen, and their students in the mid-Atlantic Coastal Plain, and range from Miocene to Pleistocene in age (Fig. 2). Formations used in this study include: Calvert Formation, Choptank Formation, St. Marys Formation, Eastover Formation, Yorktown Formation, Chowan River Formation, and Waccamaw Formation (Table 1). Specimens measured from the Calvert Formation, Choptank Formation, St. Marys Formation, Eastover Formation, and Yorktown Formation were further subdivided by member. Samples from various localities within a stratigraphic interval, when available, were kept separate during analysis to account for geographic variation (Table 2, Appendix A).

The Plum Point Marl Member of the Calvert Formation was described by Ward (1992) as being a silty sand with abundant mollusks in the sandier beds. The climate during Plum Point Marl time was warm, followed by cooling and a mass extinction (Petuch, 1997). The Boston Cliffs Member of the Choptank Formation ranges from a silty diatomaceous inner bay environment to a sandy shelly shelf environment (Ward, 1992). Cooling continued during this time. Cooling reached its peak in the inner bay environment (clay sediments with thin clayey sand beds (Blackwelder and Ward, 1976)) of the Little Cove Point Member (Ward, 1992; Petuch, 1997). A warming event occurred in the sandy-clay open-marine shelf environment found in the Windmill Point Member

| Epoch | | Formation | Member | Bed | Sampled |
|---|---|---|---|---|---|
| Pleisto-cene | | James City / Waccamaw | | | X |
| Pliocene | | Chowan River | | | X |
| | | Yorktown | Moore House | | X |
| | | | Morgart's Beach | | X |
| | | | Rushmere | | X |
| | | | Sunken Meadow | | |
| Miocene | upper | Eastover | Cobham Bay | | X |
| | | | Claremont Manor | | |
| | | St. Marys | Windmill Point | 24 | X |
| | | | Little Cove Point Beds | 21-23 | X |
| | | | Conoy | 20 | |
| | ? | Choptank | Boston Cliffs | 19 | X |
| | middle | | Drumcliff | 18 | |
| | | | St. Leonard | 17 | |
| | | Calvert | Calvert Beach | 14-16 | |
| | | | Plum Point Marl | 12-13 | |
| | | | | 10-11 | X |
| | lower | | | 4-9 | |
| | | | Fairhaven | 3b | |
| | | | | 2-3a | |
| | | | | 1 | |

Figure 2. Stratigraphic column of study area. Modified from Ward (1992) and Ward and Gilinsky (1993).

| Formation | Member | Environment |
|---|---|---|
| Waccamaw | "First Waccamaw" | Early Calabrian, first pulse of Waccamaw; more tropical than second (Petuch, 1997). |
| Chowan River | | Shallow water coarse marine sand (Ward and Blackwelder, 1987). Cooler than Morgart's Beach (Petuch, 1997). |
| Yorktown | Moore House | Lumped by Petuch (1997) as zone 2 Yorktown. Warm, nutrient-rich, quiet-water environments ending in cooling. |
| | Morgart's Beach | |
| | Rushmere | |
| Eastover | Cobham Bay | Open-marine, shallow shelf, normal salinities (Ward, 1992). Sub-tropical ending in cooling, resulting in Transmarian extinction (Petuch, 1997). |
| St. Marys | Windmill Point | Open-shelf marine (Ward, 1992). Warm-temperate to sub-tropical waters (Petuch, 1997). |
| | Little Cove Point | Inner-bay, with the exception of open-marine shell-rich beds (Ward, 1992). Water very cool, temperate endemics extinct (Petuch, 1997). |
| Choptank | Boston Cliffs | Shelly shelf sands to diatomaceous silty-clay inner bay (Ward, 1992). Cooling continues (Petuch, 1997). |
| Calvert | Plum Point Marl | Silty/Sand (Ward, 1992). Warmest Langhian climate, followed by cooling and mass extinction (Petuch, 1997). |

Table 1. Formations and Members used in this study.

| Formation | Member | Taxon | Locality | n |
|---|---|---|---|---|
| Waccamaw | | *C. conradi* | Old Dock | 14 |
| Chowan River | | *C. conradi* | Above Edenhouse | 12 |
| | | *C. conradi* | Mt. Gould | 23 |
| | | *C. conradi* | Colerain | 21 |
| | | *C. conradi* | Gomez Pit | 23 |
| Yorktown | Moore House | *C. conradi* | 1/2 mi Ab Ft. Boykin | 23 |
| | | *C. inaequalis* | Ft. Boykin | 12 |
| | Morgart's Beach | *n/a* | No sample | n/a |
| | Rushmere | *C. inaequalis* | Day's Pt 6' Ab Base | 18 |
| | | *C. inaequalis* | Old Sparta | 14 |
| Eastover | Cobham Bay | *n/a* | No sample | n/a |
| St. Marys | Windmill Point | *C.inaequalis* | Combined Locations | 15 |
| | Little Cove Point | *C. inaequalis* | Combined Locations | 20 |
| Choptank | Boston Cliffs | *C. inaequalis* | Boston Cliffs | 9 |
| Calvert | Plum Point Marl | *C. inaequalis* | Between Will. & C.R. | 9 |

A.

| Formation | Member | Taxon | Locality | n |
|---|---|---|---|---|
| Waccamaw | | *P. multilineata* | Old Dock | 9 |
| Chowan River | | *P. crenulata* | Below Hamilton | 33 |
| | | *P. crenulata* | Gomez Pit Upper | 20 |
| | | *P. crenulata* | Colerain | 22 |
| | | *P. crenulata* | Above Edenhouse | 16 |
| | | *P. multilineata* | Colerain | 11 |
| Yorktown | Moore House | *P. multilineata* | 1/2 mi Ab Ft. Boykin | 11 |
| | | *P. crenulata* | Ft. Boykin | 23 |
| | | *P. crenulata* | Chuckatuck Pit | 20 |
| | Morgart's Beach | *P. crenulata* | Below Ft. Boykin | 20 |
| | Rushmere | *P. crenulata* | Day's Point | 33 |
| | | *P. crenulata* | Old Sparta | 23 |
| | | *P. crenulata* | Rushmere Wharf | 11 |
| Eastover | Cobham Bay | *P. crenulata* | Combined Locations | 25 |
| St. Marys | Windmill Point | n/a | No sample | n/a |
| | Little Cove Point | *P. crenulata* | Combined Locations | 38 |
| Choptank | Boston Cliffs | n/a | No sample | n/a |
| Calvert | Plum Point Marl | *P. prunus* | Between Will. & C.R. | 30 |
| | | *P. crenulata* | Between Will. & C.R. | 12 |

B.

Table 2. Species, locations, and sample sizes for: A. *Caryocorbula* and B. *Parvilucina*. Location data are located in Appendix A.

(Ward, 1992; Petuch, 1997). Warm open-marine environments persisted into the fine to medium-grained shelly sand Cobham Bay Member, which ended in a cooling event (Ward, 1992; Ward and Blackwelder, 1976; Petuch, 1997). Warm, nutrient-rich waters were common in the Yorktown Formation, followed by a cooling event (Petuch, 1997). The Chowan River Formation represents a shallow sea that was slightly cooler than that found during Morgart's Beach time (Ward and Blackwelder, 1987; Petuch, 1997). The Waccamaw Formation was deposited in tropical marine environment (Petuch, 1997). The Miocene section displays within-habitat time averaging (Kidwell, 1989).

Two species of *Caryocorbula* (*C. inaequalis* and *C. conradi*) and three species of *Parvilucina* (*P. prunus*, *P. crenulata*, and *P.multilineata*) were used in this study (Table 2). The genera were chosen for their long stratigraphic range. Specimens ranging in size classes from juvenile to adult were measured in this study (based upon presumed adult length given by Campbell (1993)). Corbulid valves often exfoliate along internal conchiolin layers. Exfoliated valves were not measured in this study, as doing so would artificially inflate internal volume values and artificially decrease thickness values.

Three measurements were made on all valves: length, valve thickness, and internal volume. Length was measured as the maximum distance from the posterior margin to the anterior margin. Valve thickness was measured at a standard site located on the pallial line midway between the anterior and posterior margin. Length and thickness measurements were made with digital calipers (± 0.01mm). Internal volume was measured by filling the valve with sand. Being careful not to compact the sand, as this could lead to overestimation of internal volume and damage the valve, the sand was then weighed on an AccuLab VI-1mg electronic balance with a readability of 0.001 g.

Knowing the density of the sand (1.54 g/ml), mass was converted to volume, revealing the internal volume of the bivalve valve. The sand used in this study was collected from eolian dunes at the south end of Wrightsville Beach, NC. The sand was dry-sieved. Sand from the size-80 (0.177 mm) sieve was used in this study.

An individual *Caryocorbula inaequalis* from the Plum Point Marl Member was used to test repeatability of length, thickness, and internal volume measurements. The individual was measured for each parameter ten times. Variability in each parameter was calculated as the difference between the maximum and minimum value as a proportion of the mean value. Variability in length was ± 0.29%. Variability in thickness was ± 2.3%. Variability in internal volume was ± 6.1%. The high value of variability in internal volume is initially troubling. One might expect this high amount of variability to result in excessive variation from the trend line when correlating internal volume with length, resulting in an inaccurate description of the relationship between the two parameters. This, however, is not the case. Correlations of internal volume and length display higher $R^2$ values than correlations of thickness and length. For example, the regression of internal volume on length for the smallest genus (*Parvilucina*) with the smallest sample size (n=9) from the Waccamaw Formation yields an $R^2$ value of 0.9414.

Valve length, valve thickness, and internal volume data from each species and each sample were log-transformed due to the allometric growth of these bivalves. Thickness and internal volume log-transformed data were each regressed on log-transformed length for each species from each stratigraphic interval. A major axis (geometric mean) regression (Sokal and Rohlf, 1995) was performed using Microsoft Excel software. A model II regression was utilized because the data did not fit the

assumptions required for a model I linear regression. Both variables were subject to error and were not independent of each other. This regression analysis produced an equation that described the relationship between thickness and length and internal volume and length.

The standard length was inserted into each equation to determine thickness and internal volume for each species at each stratigraphic interval (keeping individual localities separate). The standard length was defined as the mean of mean lengths at each stratigraphic interval, and was calculated for each genus. Cost-benefit ratio was calculated by dividing resulting thickness values by resulting internal volume values in order to compare overall attractiveness of prey to naticid predators (based upon thickness and internal volume) among stratigraphic intervals. Geographic variability was calculated where multiple samples were available from a single stratigraphic interval. Geographic variability was calculated as the difference between minimum and maximum values divided by the average value (Kelley, 1989). In order for the temporal change in thickness, internal volume, and cost-benefit ratio values to be considered significant, net change through the section should be substantially greater than the variation found in repeatability and geographic variation that existed at any one time. Temporal change considered insignificant should be substantially less than geographic variation at one time. Temporal change that approximated geographic variation was treated as insignificant in this study. Spearman's Rank Correlation Coefficient was calculated for thickness, internal volume, and cost-benefit ratio values at the standard length to determine if a relationship existed between these values and their stratigraphic order to determine if evolution occurred in a gradual mode (i.e. directional trend) (Kelley, 1989).

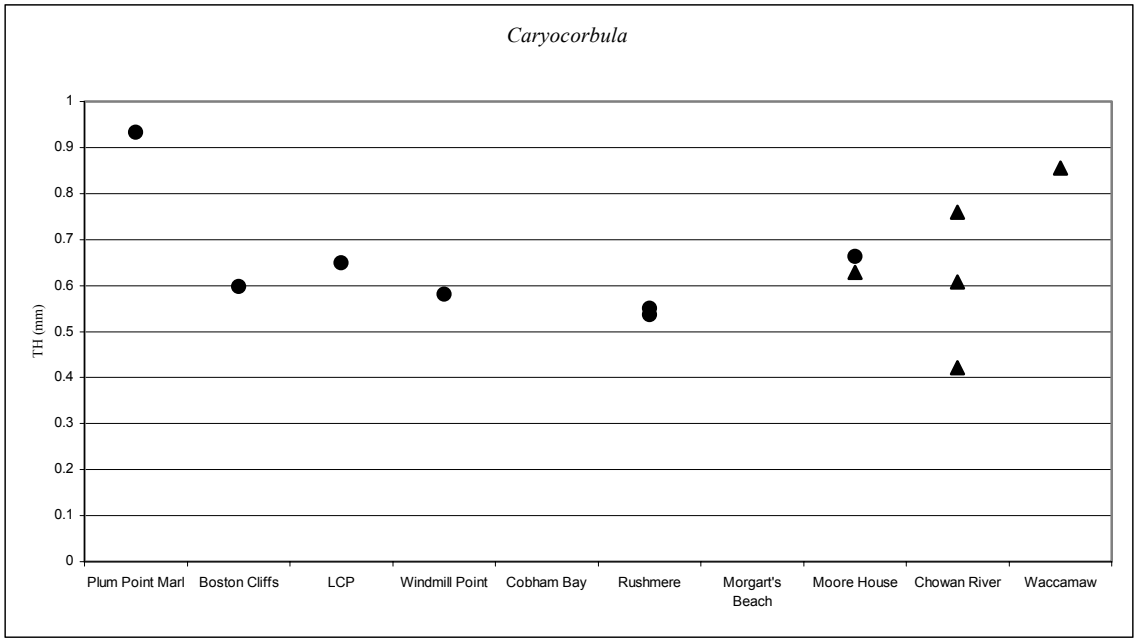
Drilling frequency was calculated for prey species from each stratigraphic interval by dividing the number of drilled valves by half the total number of valves, as it takes one drilled valve to kill a two-valved animal. This method was chosen because it is the most statistically sound and does not artificially inflate the sample size (Bambach and Kowalewski, 2000). Prey effectiveness was calculated by dividing the number of incomplete drill holes by the total number of attempted drill holes (Kelley et al., 2001). Drilling frequency and prey effectiveness were calculated for each species at each stratigraphic interval and locality (when available) from Kelley and Hansen's datasheets. Drilling frequency was compared to thickness, internal volume, and cost-benefit ratio using a least-squares regression for each genus to determine the relationship between the evolution of anti-predatory morphologies and predation intensity. Prey effectiveness was compared to thickness, internal volume, and cost-benefit ratio using a least-squares regression for each genus to determine if the evolution of anti-predatory morphologies affected prey effectiveness.

# RESULTS

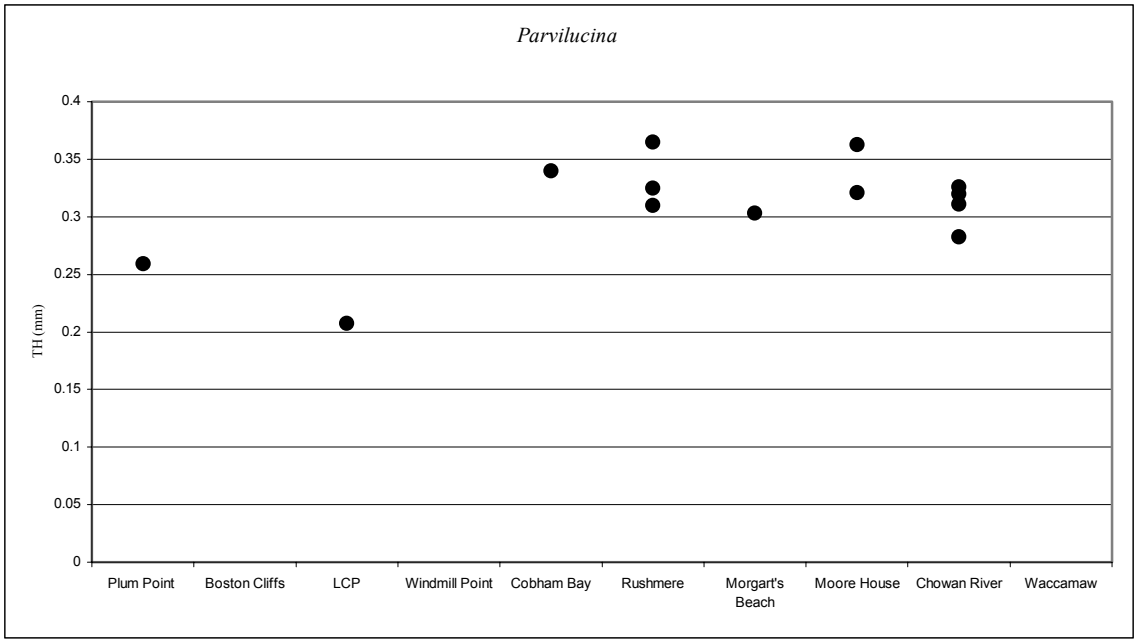
## Thickness

*Caryocorbula inaequalis* displayed a thickness at the standard length of just less than one mm (0.93mm) in the Plum Point Marl (Fig. 3). Thickness decreased to 0.60 mm in the Boston Cliffs Member. Thickness remained at similar values through the Little Cove Point Member (0.65mm), Windmill Point Member (0.58mm), Rushmere Member (0.54mm and 0.55mm), and Moore House Member (0.66mm). The percent difference in thickness of *C. inaequalis* between the Plum Point Marl and the Moore House Member was –28.95% (Table 3). Geographic variation of thickness in *C. inaequalis* was 2.60% in the Rushmere Member. The temporal decrease in thickness was significantly greater than the geographic variation at one time, but because it was in the opposite direction of what was predicted it did not support the hypothesis. The Spearman's Rank Correlation Coefficient for thickness and stratigraphic order for *C. inaequalis* was S=-0.371 (p=0.468). This nonsignificant correlation suggests that a directional trend did not occur.

*C. conradi* displayed a thickness at the standard length of 0.63 mm in the Moore House Member (Fig. 3). Thickness values for *C. conradi* decreased slightly on average to 0.60 mm in the Chowan River Formation, though there was a large amount of geographic variation (0.42 mm-0.76 mm). Thickness increased in the Waccamaw Formation to 0.86 mm. The percent difference in thickness of *C. conradi* between the Moore House Member and the Waccamaw Formation was 35.90% (Table 3). Geographic variation of thickness in *C. conradi* was 25.37%. The temporal increase in




A.




B.

Figure 3. Thickness graph for: A. *Caryocorbula* (circles: *C. inaequalis*; triangles: *C. conradi*) and B. *Parvilucina crenulata*. Stratigraphic intervals arranged in order of decreasing age from left to right.

| *Caryocorbula inaequalis* | TH | IV | CB |
|---|---|---|---|
| Overall Change | -28.95% | -0.66% | -28.47% |
| Geographic Variation | 2.60% | 8.50% | 11.50% |
| Significant Overall Change? | Yes | No | Yes |
| Spearman S | -0.371 | -0.314 | -0.314 |
| p-value | 0.468 | 0.544 | 0.544 |
| Support Hypothesis? | No | No | No |

A.

| *Caryocorbula conradi* | TH | IV | CB |
|---|---|---|---|
| Overall Change | 35.90% | -25.81% | 83.19% |
| Geographic Variation | 25.37% | 24.77% | 67.88% |
| Significant Overall Change? | Yes | No | Yes |
| Spearman S | 0.500 | -1.00 | 1.00 |
| p-value | 0.667 | <<0.05 | <<0.05 |
| Support Hypothesis? | Yes | No | Yes |

B.

| *Parvilucina crenulata* | TH | IV | CB |
|---|---|---|---|
| Overall Change | 19.58% | -17.17% | 45.26% |
| Geographic Variation | 12%-16% | 6%-24% | 12%-21% |
| Significant Overall Change? | No | No | Yes |
| Spearman S | 0.536 | -0.643 | 0.821 |
| p-value | 0.215 | 0.119 | 0.023 |
| Support Hypothesis? | No | No | Yes |

C.

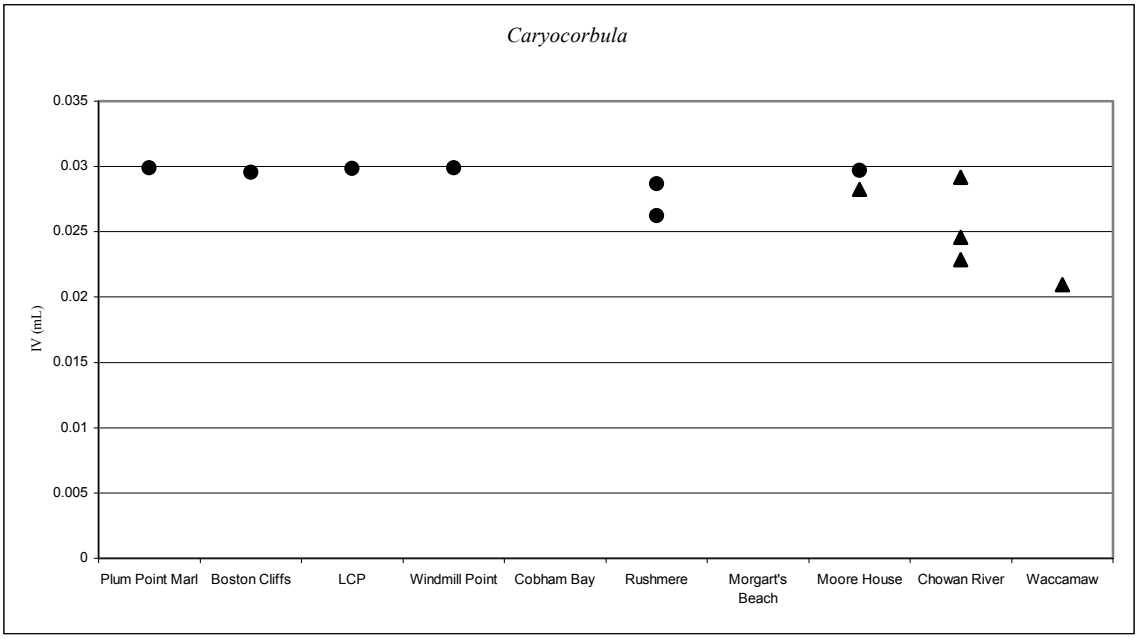
Table 3. Morphologic trends for: A *Caryocorbula inaequalis*, B. *C. conradi*, and C. *Parvilucina crenulata*. TH = thickness, IV = internal volume, and CB = cost-benefit ratio.

thickness was significantly greater than the geographic variation, and did support the hypothesis. Spearman's S between thickness and stratigraphic order was S=0.500 (p=0.667). This trend is nonsignificant because there are only three samples.

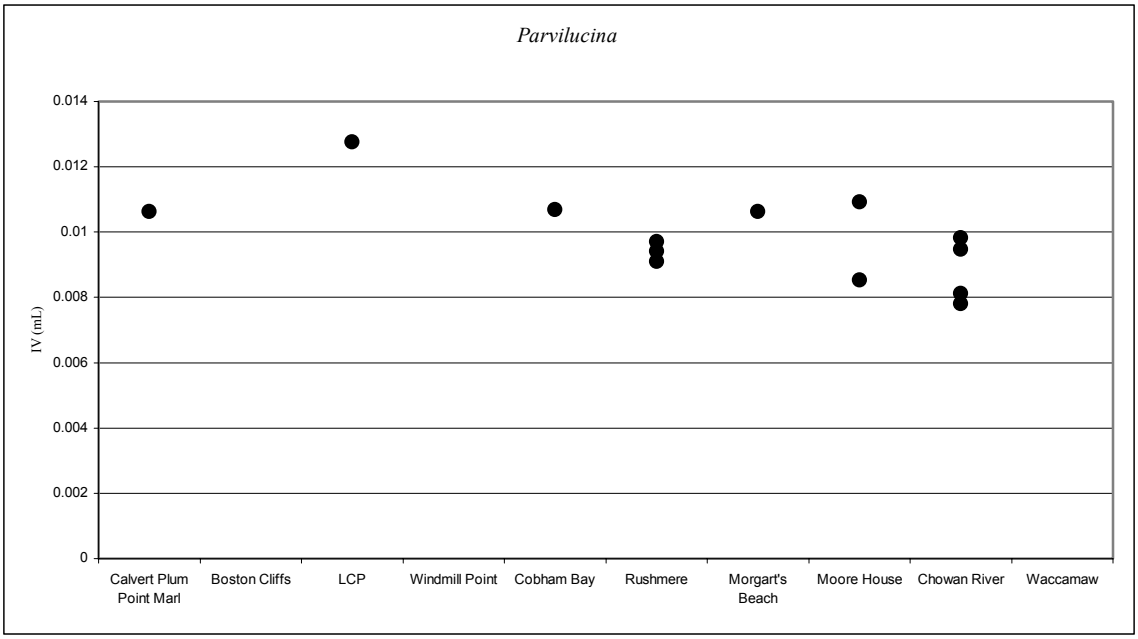
*Parvilucina crenulata* displayed a thickness of 0.26 mm in the Plum Point Marl (Fig. 3). Thickness decreased to 0.21 mm in the Little Cove Point Member and increased to 0.34 mm in the Cobham Bay Member. Thickness values fluctuated but remained relatively high in the Rushmere Member (0.31 mm-0.36 mm), Morgart's Beach Member (0.30 mm), Moore House Member (0.30 mm-0.36 mm), and the Chowan River Formation (0.28 mm-0.32 mm). Thickness values of *P. prunus* and *P. multilineata* were within the range of thickness values of *P. crenulata*, but were not analyzed for evolutionary trends due to low sample numbers. The percent difference of thickness in *P. crenulata* from the Plum Point Member to the Chowan River Formation was 19.58% (Table 3). Geographic variation was high in *P. crenulata*, ranging from 12% to 16%. The temporal increase in thickness was just slightly greater than geographic variation; therefore the temporal change in thickness was not interpreted as significant. This nonsignificant change did not support the hypothesis, but the change was in the direction predicted.

Internal Volume

*Caryocorbula inaequalis* displayed little variation in internal volume at the standard length in the Plum Point Marl (0.0299 ml), Boston Cliffs Member (0.0296 ml), Little Cove Point Member (0.0299 ml), and Windmill Point Member (0.0299 ml) (Fig. 4). Internal volume values decreased slightly in the Rushmere Member (0.0262 ml and




A.




B.

Figure 4. Internal volume graph for: A. *Caryocorbula* (circles: *C. inaequalis*; triangles: *C. conradi*) and B. *Parvilucina crenulata*. Stratigraphic intervals arranged in order of decreasing age from left to right.

0.0287 ml for two localities) and rose slightly in the Moore House Member (0.0282 ml and 0.0297 ml for two localities). The percent difference of internal volume in *C. inaequalis* between the Plum Point Marl and the Moore House Member was –0.66% (Table 3). Geographic variation of internal volume in *C. inaequalis* was 8.50%. The temporal change of internal volume was much less than the geographic variation at one time, and did not support the hypothesis.

Internal volume at the standard length for *Caryocorbula conradi* in the Moore House Member was 0.0282 ml (Fig. 4). Internal volume decreased in the Chowan River to an average of 0.0255 ml, though values ranged from 0.0228 ml to 0.0292 ml. Internal volume decreased further in the Waccamaw Formation to 0.0209 ml. The percent difference of internal volume in *C. conradi* from the Moore House Member to the Waccamaw Formation was -25.81% (Table 3). Geographic variation of internal volume in *C. conradi* was 24.77%. The temporal change in internal volume was comparable to the geographic variation, and did not support the hypothesis (though change occurred in the predicted direction).

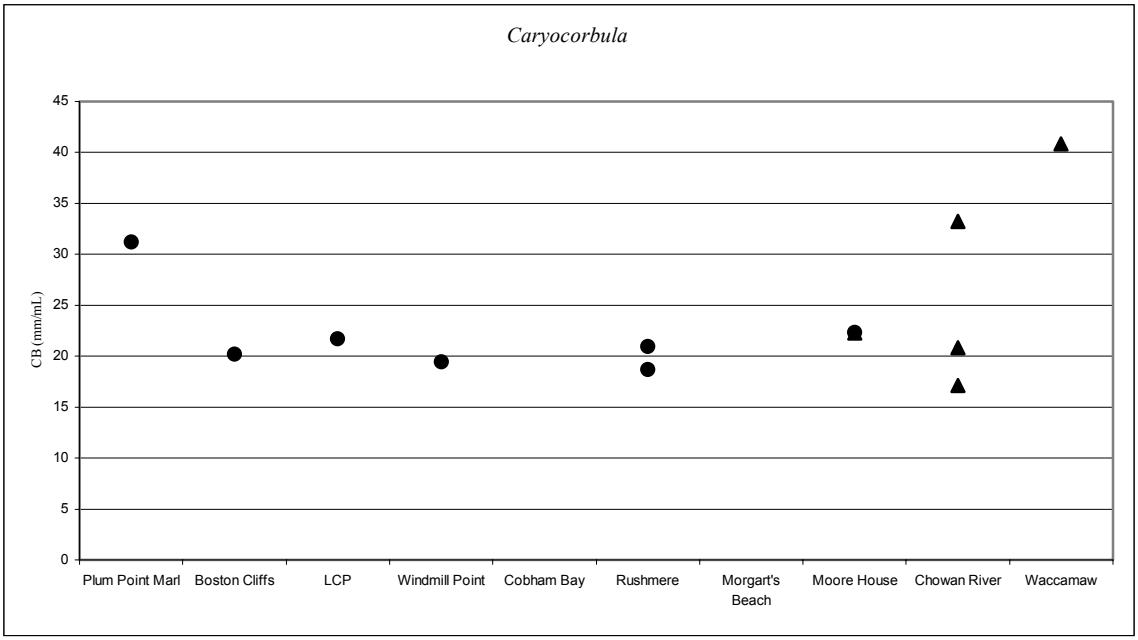
*Parvilucina crenulata* displayed an internal volume at the standard length of 0.0106 ml in the Plum Point Marl (Fig. 4). Internal volume increased in the Little Cove Point Member to 0.0128 ml and decreased in the Cobham Bay Member to 0.0107 ml. The decrease in internal volume continued in the Rushmere Member with an average value of 0.0094 ml (0.0091 ml, 0.0094 ml, and 0.0097 ml for the three localities). Internal volume fluctuated in the Morgart's Beach Member (0.0106 ml), Moore House Member (0.0085 ml and 0.0109 ml for two localities), and Chowan River Formation (0.0078 ml, 0.0081 ml, 0.0095 ml, and 0.0098 ml for four localities). The percent

difference of internal volume in *P. crenulata* between the Plum Point Marl and the Chowan River Formation was –17.17% (Table 3). Geographic variation ranged between 6% and 24%. Temporal change of internal volume in *P. crenulata* was not significant in comparison to the geographic variation, and did not support the hypothesis (though change occurred in the predicted direction).

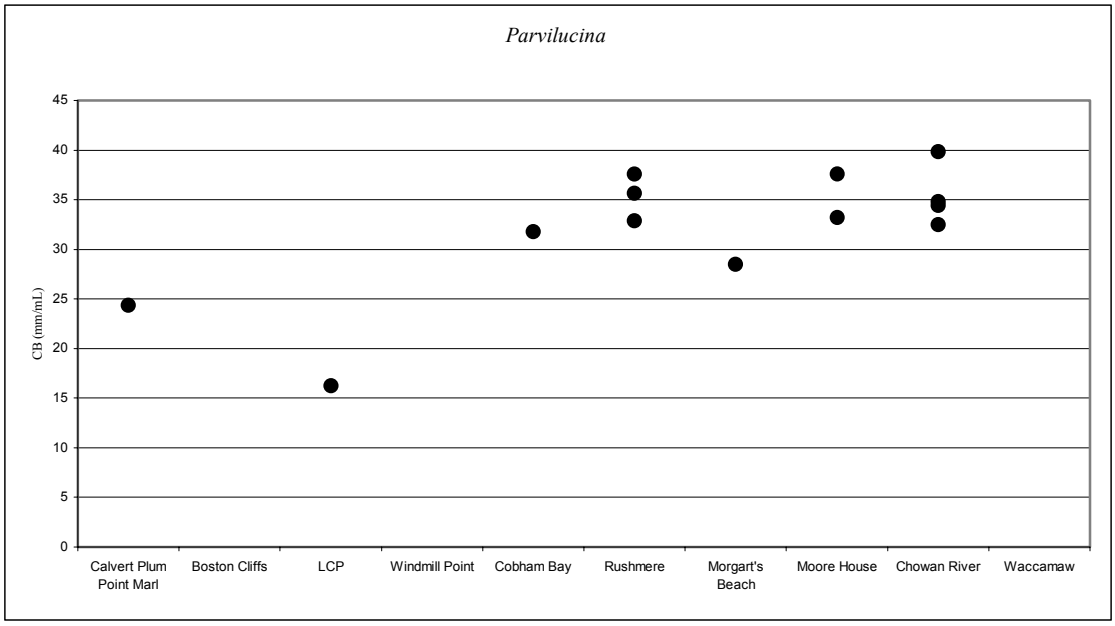
Cost-Benefit Ratio

*Caryocorbula inaequalis* displayed a cost-benefit ratio value at the standard length of 31.21 mm/ml in the Plum Point Marl (Fig. 5). Cost-benefit ratio decreased in the Boston Cliffs Member to 20.22 mm/ml. *C. inaequalis* cost-benefit ratio values remained low through the Little Cove Point Member (21.74 mm/ml), Windmill Point Member (19.45 mm/ml), and Rushmere Member (18.70 mm/ml and 20.98 mm/ml for the two localities). The percent difference of cost-benefit ratio in *C. inaequalis* between the Plum Point Marl and the Rushmere Member was -28.47% (Table 3). Geographic variation of cost-benefit ratio was 11.50%. The temporal decrease of cost-benefit ratio in *C. inaequalis* was significantly greater than the geographic variation, and did not support the hypothesis because it was in the direction opposite of what was predicted.

Cost-benefit ratio at the standard length for *Caryocorbula conradi* in the Moore House Member was 22.29 mm/ml (Fig. 5). The cost-benefit ratio values increased on average in the Chowan River Formation to 23.72 mm/ml (17.12 mm/ml, 20.84 mm/ml, and 33.23 mm/ml for the three localities), and increased in the Waccamaw Formation (31.21 mm/ml). The percent difference of cost-benefit ratio in *C. conradi* from the




A.




B.

Figure 5. Cost-benefit ratio graph for: A. *Caryocorbula* (circles: *C. inaequalis*; triangles: *C. conradi*) and B. *Parvilucina crenulata*. Stratigraphic intervals arranged in order of decreasing age from left to right.

Moore House Member to the Waccamaw Formation was 83.19% (Table 3). Geographic variation was 67.88%. The temporal increase of cost-benefit ratio in *C. conradi* was significant, and did support the hypothesis. The Spearman's correlation coefficient between cost-benefit ratio and stratigraphic order was S=1.00 ($p<<0.05$), and suggests a gradual mode of evolution (although there were only three data points).

Cost-benefit ratio at the standard length for *Parvilucina crenulata* in the Plum Point Marl was 24.37 mm/ml (Fig. 5). Cost-benefit ratio decreased in the Little Cove Point Member to 16.27 mm/ml. The cost-benefit ratio values increased in the Cobham Bay Member to 31.78 mm/ml, and cost-benefit ratio remained high in the Rushmere Member (32.91 mm/ml, 35.67 mm/ml, and 37.57 mm/ml for the three localities), Morgart's Beach Member (28.47 mm/ml), Moore House Member (33.21 mm/ml and 37.61 mm/ml for the two localities), and Chowan River Formation (32.51 mm/ml, 34.43 mm/ml, 34.81 mm/ml, and 39.82 mm/ml for the four localities). The percent difference of cost-benefit ratio in *P. crenulata* between the Plum Point Marl and the Chowan River Formation was 45.26% (Table 3). Geographic variation of cost-benefit ratio was 12%-21%. The temporal increase of cost-benefit ratio in *P. crenulata* was significantly greater than the geographic variation, and did support the hypothesis. The Spearman's correlation coefficient between cost-benefit ratio and stratigraphic order was S=0.821 ($p=0.023$), and suggests that evolution was in a gradual mode.

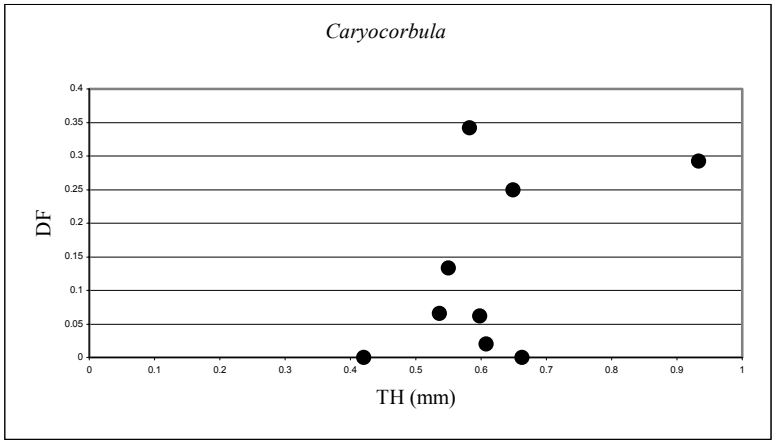
Drilling Frequency and Anti-Predatory Morphology

The least-squares regression between drilling frequency and thickness at the standard length for *Caryocorbula* was R=0.507 (p=0.163) (Fig. 6). The regression between drilling frequency and internal volume at the standard length was R=0.433 (p=0.244). The regression between drilling frequency and cost-benefit ratio at the standard length was R=0.465 (p=0.207). There were no significant correlations found between drilling frequency and thickness, internal volume, nor cost-benefit ratio at the standard length in *Caryocorbula*. Drilling frequencies in *Caryocorbula* fluctuated, but were generally high in the Miocene and low in the Pliocene and Pleistocene (Fig. 7).

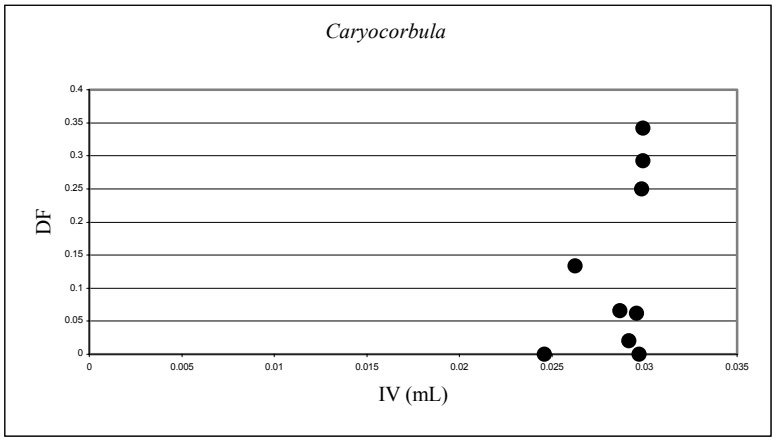
The least-squares regression between drilling frequency and thickness at the standard length for *Parvilucina* was R=0.095 (p=0.768) (Fig. 8). The regression between drilling frequency and internal volume at the standard length was R=0.483 (p=0.112). The regression between drilling frequency and cost-benefit ratio at the standard length was R=0.445 (p=0.147). There were no significant correlations found between drilling frequency and thickness, internal volume, or cost-benefit ratio at the standard length in *Parvilucina*. Drilling frequencies fluctuated throughout the history of *Parvilucina* (Fig. 7).

Prey Effectiveness and Anti-Predatory Morphology

The least-squares regression between prey effectiveness and thickness at the standard length for *Caryocorbula* was R=0.506 (p=0.164) (Fig. 9). The regression between prey effectiveness and internal volume at the standard length was R=0.518 (p=0.153). The regression between prey effectiveness and cost-benefit ratio at the




A.

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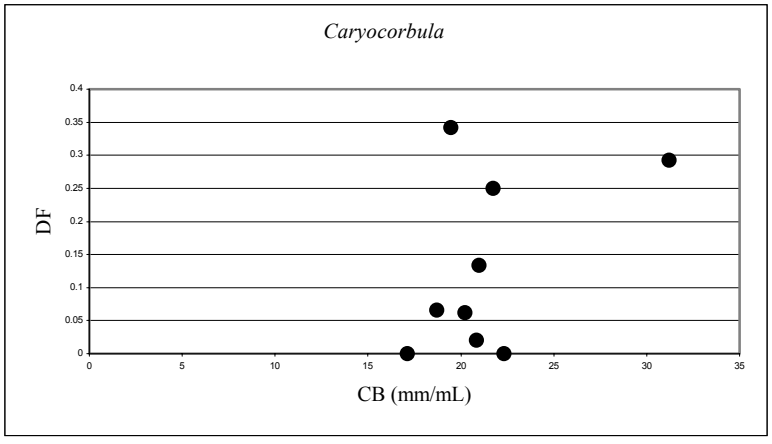
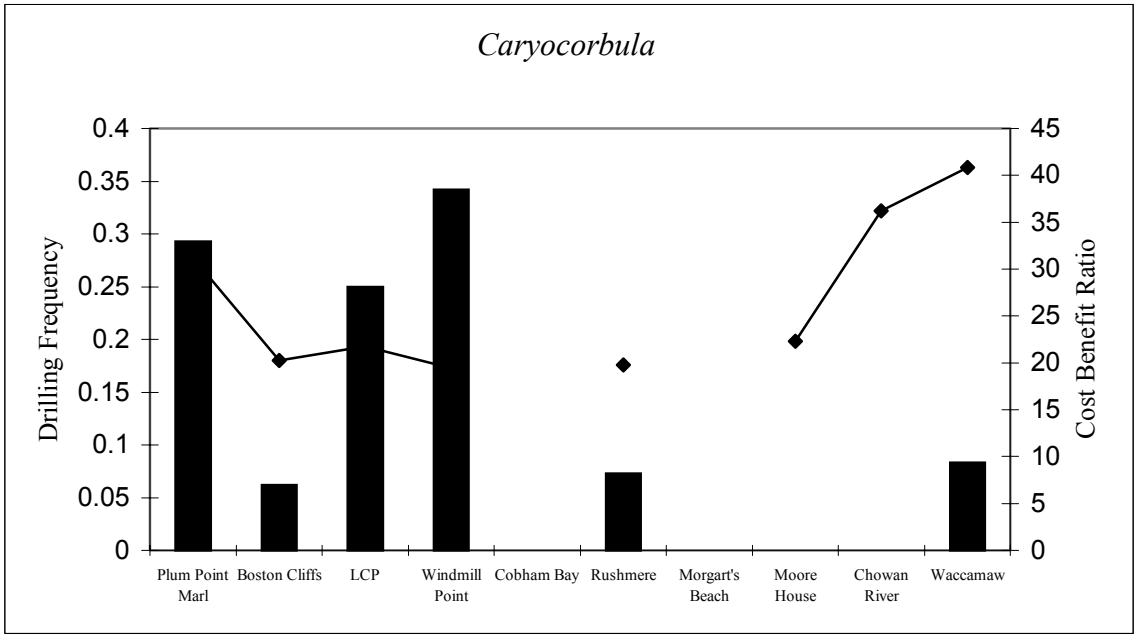
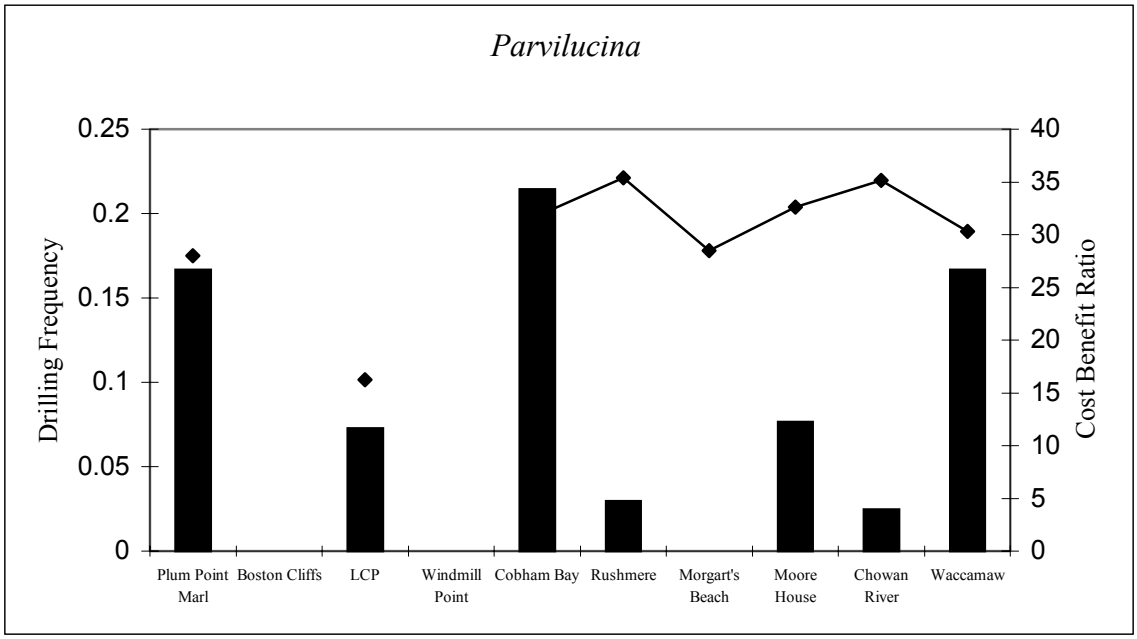



C.

Figure 6. Scatter plots for *Caryocorbula* of: A. drilling frequency and thickness (R=0.507, p=0.163), B. drilling frequency and internal volume (R=0.433, p=0.244), and C. drilling frequency and cost-benefit ratio (R=0.465,p=0.207).

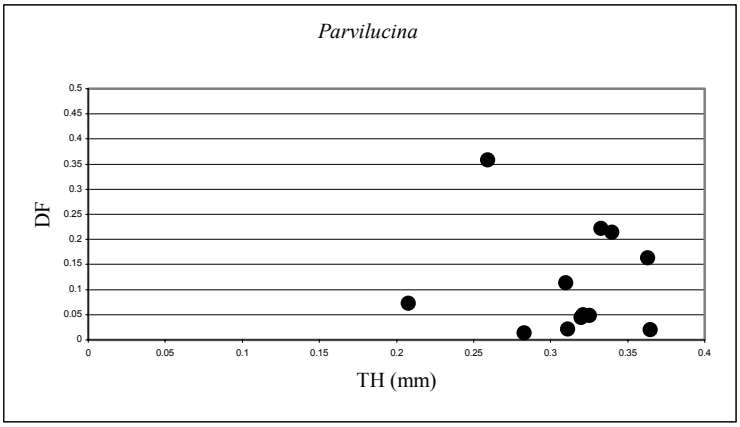



A.

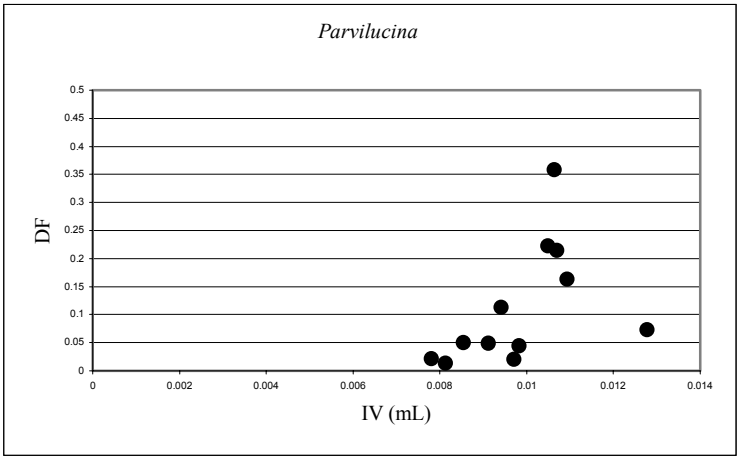



B.

Figure 7. Drilling frequencies (bars) and cost-benefit ratio at the standard length (points) of: A. *Caryocorbula* and B. *Parvilucina*. Drilling frequencies for this figure were calculated at the genus level for each stratigraphic interval. Stratigraphic intervals arranged in order of decreasing age from left to right.




A.

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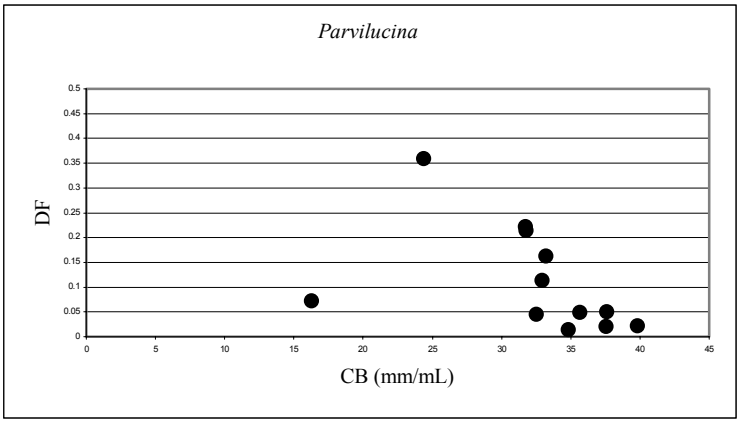
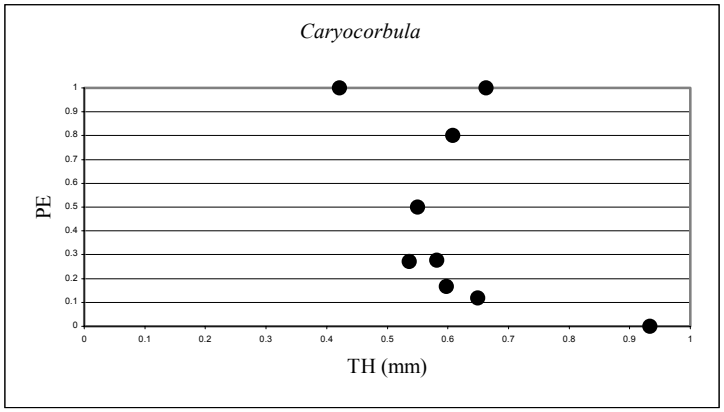
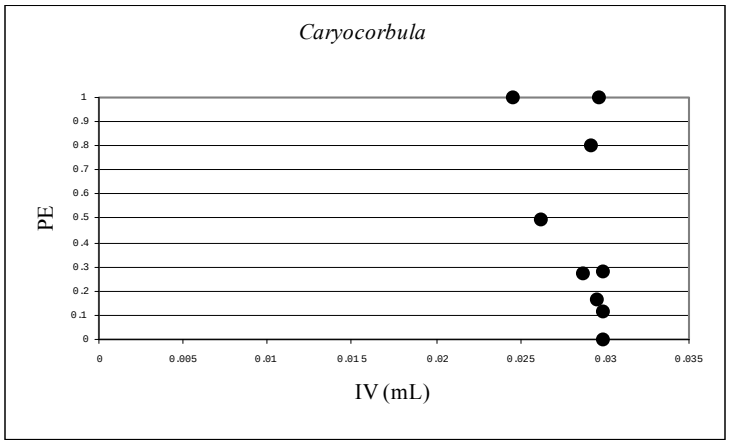



C.

Figure 8. Scatter plots for *Parvilucina* of: A. drilling frequency and thickness (R=-0.095, p=0.768), B. drilling frequency and internal volume (R=0.483, p=0.112), and C. drilling frequency and cost-benefit ratio (R=-0.445,p=0.147).




A.

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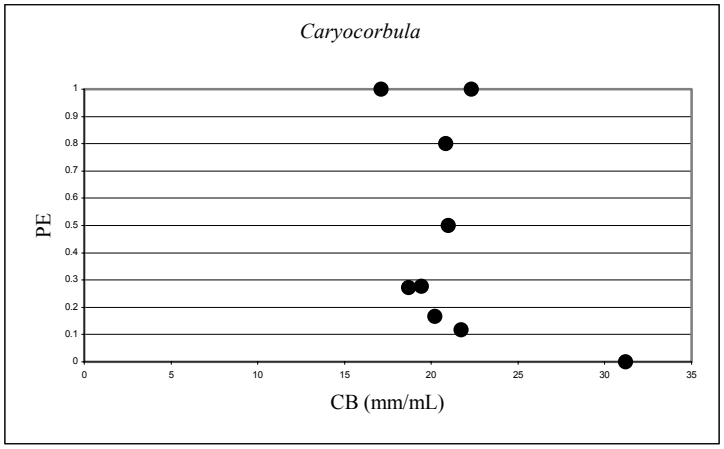
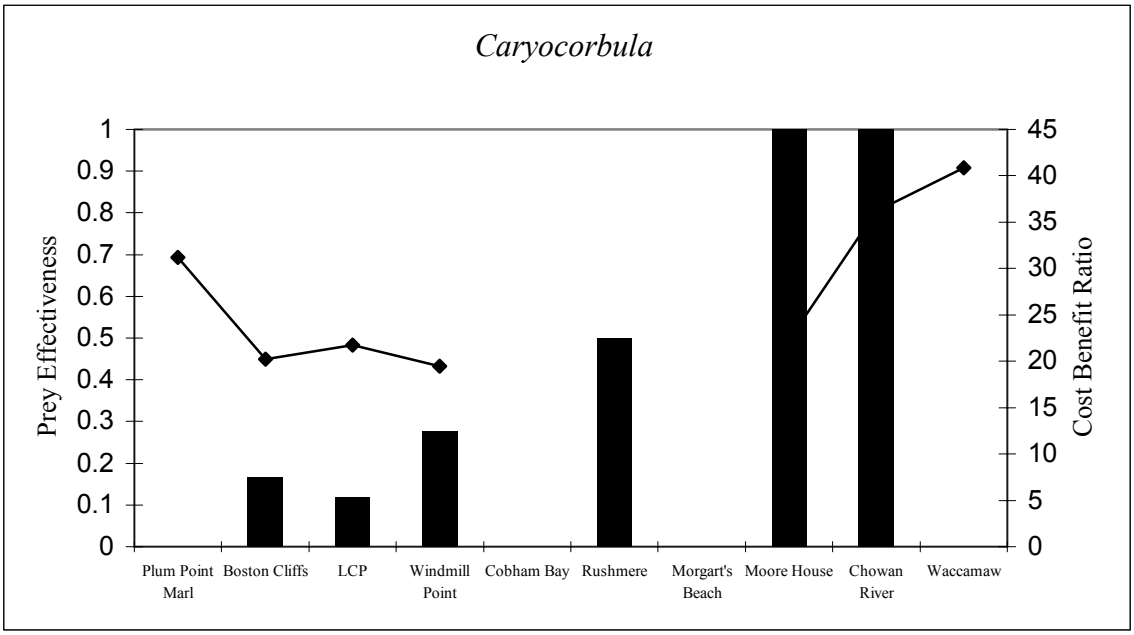



C.

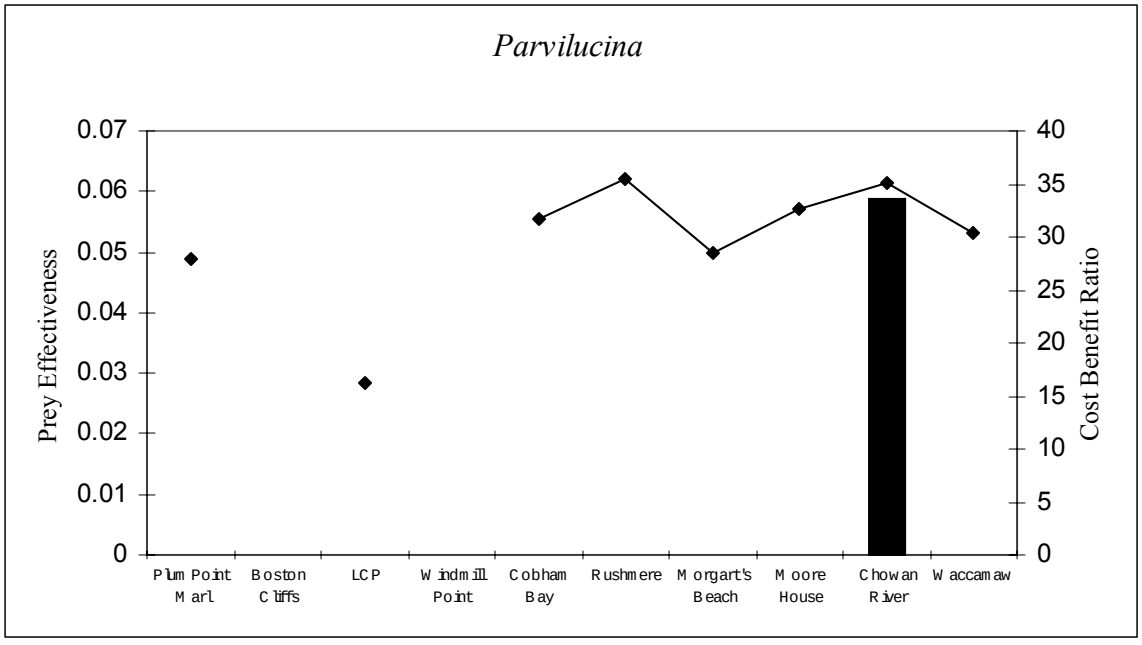
Figure 9. Scatter plots for *Caryocorbula* of: A. prey effectiveness and thickness (R=-0.506, p=0.164), B. prey effectiveness and internal volume (R=-0.518, p=0.153), and C. prey effectiveness and cost-benefit ratio (R=-0.441,p=0.234).

standard length was R=0.441 (p=0.234). There were no significant correlations found between prey effectiveness and thickness, internal volume, or cost-benefit ratio at the standard length in *Caryocorbula*. Prey effectiveness displayed an increase from the Plum Point Marl to the Chowan River Formation, and decreased sharply in the Waccamaw Formation similar to the results predicted by the Kelley-Hansen model of escalation for the faunal level (Fig. 10).

The least-squares regression between prey effectiveness and thickness at the standard length for *Parvilucina* was R=0.204 (p=0.524) (Fig. 11). The regression between prey effectiveness and internal volume at the standard length was R=0.391 (p=0.209). The regression between prey effectiveness and cost-benefit ratio at the standard length was R=0.121 (p=0.708). There were no significant correlations found between prey effectiveness and thickness, internal volume, or cost-benefit ratio at the standard length in *Parvilucina*, but this is not surprising as there were hardly any incomplete drill holes. Prey effectiveness values were consistently low throughout the history of *Parvilucina* (Fig. 10).

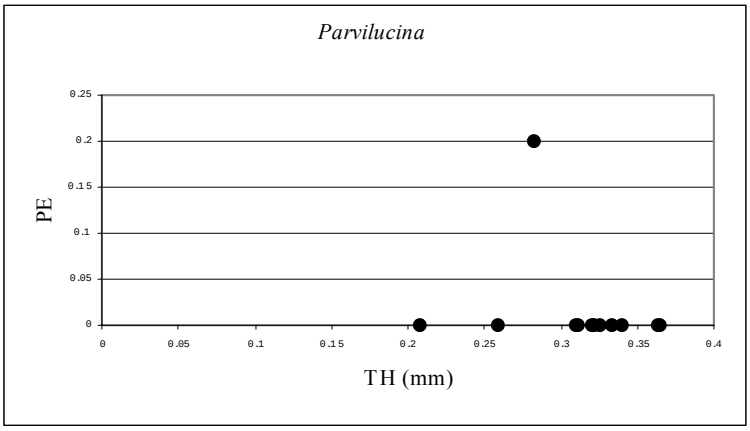



A.

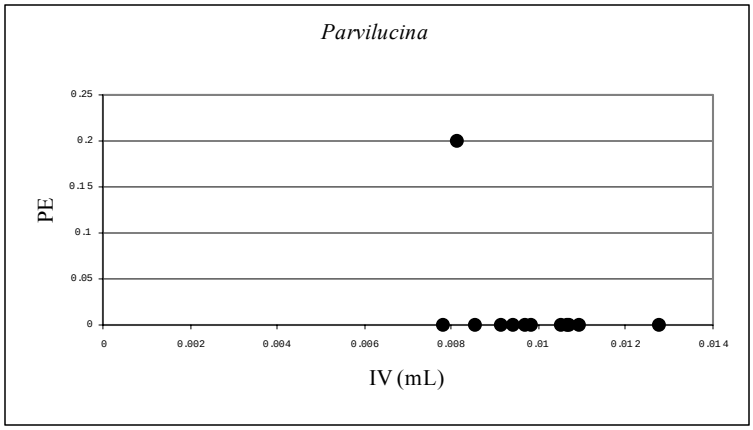



B.

Figure 10. Prey effectiveness (bars) and cost-benefit ratio at the standard length (points) of: A. *Caryocorbula* and B. *Parvilucina*. Prey effectiveness for this figure was calculated at the genus level for each stratigraphic interval. Stratigraphic intervals arranged in order of decreasing age from left to right.




A.

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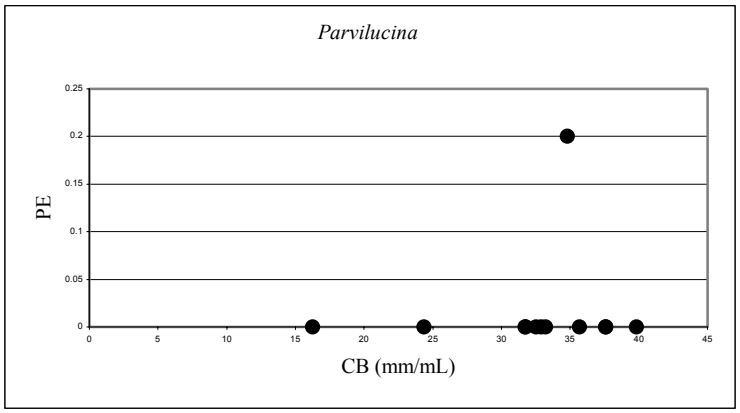


C.

Figure 11. Scatter plots for *Parvilucina* of: A. prey effectiveness and thickness (R=0.204, p=0.524), B. prey effectiveness and internal volume (R=0.391, p=0.209), and C. prey effectiveness and cost-benefit ratio (R=0.121,p=0.708).

# DISCUSSION

## Anti-Predatory Morphology Through Time

Thickness of *Caryocorbula inaequalis* at the standard length decreased significantly through time in comparison with geographic variation at one time. This decrease in thickness does not support the hypothesis that anti-predatory traits should become better expressed with time. Internal volume of *C. inaequalis* showed no significant change in comparison with geographic variation. While this result does not support the hypothesis that anti-predatory traits should become better expressed with time, it is not surprising in that Kelley (1989) found that non-directional fluctuation characterized the evolution of internal volume in Miocene Chesapeake Group bivalves. When the thickness and internal volume are compared simultaneously as cost-benefit ratio, values decreased significantly through time. This result means that the overall morphologic attractiveness of *C. inaequalis* increased with time, contrary to my prediction.

*Caryocorbula conradi* thickness values increased significantly through time in comparison with geographic variation. Internal volume decreased greatly in the predicted direction, though the decrease was not significant in comparison with geographic variation. Cost-benefit ratio values showed a significant increase despite tremendous geographic variation (68%). Cost-benefit ratios evolved in a gradual mode as indicated by the significant Spearman's correlation between cost-benefit ratio and stratigraphic order. This significant correlation is surprising since Spearman's correlation between thickness and stratigraphic order suggests evolution in a non-gradual mode. This result

suggests that tracing the evolution of a few characters individually may not be sufficient to determine the evolutionary strategies of an organism.

*Parvilucina crenulata* thickness values increased 20%, though this was not interpreted as significant when compared to geographic variation. Similar nonsignificant trends were found in internal volume, which decreased by 17%. Valve thickness and internal volume both showed trends in the direction predicted by the hypothesis; however, neither resulted in significant changes when evaluated individually. The results were different when the sum changes of thickness and internal volume were considered together as cost-benefit ratio. Cost-benefit ratio at the standard length displayed a significant increase of 45% (nearly double the geographic variation). The evolution of cost-benefit ratio occurred in a gradual mode, as indicated by the significant Spearman's correlation between cost-benefit ratio and stratigraphic interval. Evolution of thickness and internal volume, examined individually, did not occur in a gradual mode. Once again, we see that examining the evolution of characters individually may not give an accurate impression of what is occurring evolutionarily. We see that trends (that are not clearly significant) evolving in a fluctuating manner can have the sum effect of significant gradual evolution. This case of the whole being greater than the sum of its parts is likely true because nature selects for naticids that prey on clams with the lowest cost-benefit ratio, which incorporates both thickness and internal volume.

Kelley and Hansen (2001) found that predation-related characters displayed a greater magnitude of change and higher frequency of gradual evolution within species than did non-predation-related characters (42% vs. 13%, respectively) (Table 4). While this study did not examine non-predation-related characters, it did find that gradual

| | | Gradual Evolution | Punctuational Evolution |
|---|---|---|---|
| This Study (Predation-related) | | 3 | 6 |
| Kelley and Hansen (2001) | Predation-related | 10 | 14 |
| | Non-predation-related | 9 | 61 |

Table 4. Mode of evolution for predation- and non-predation-related characters in bivalve species. Punctuational evolution is defined here as stasis or non-directional fluctuation.

evolution was not uncommon in predation-related characters (33%). Gould (1990) predicted that trends produced by natural selection would take place on time scales too short in duration to be seen in the fossil record. These results suggest that selection by naticid predators influenced anti-predatory morphology in their prey, and that natural selection can produce trends seen in geologic time.

Did the Evolution of Anti-Predatory Morphology Affect Predation Intensity?

When comparing drilling frequency to thickness, internal volume, and cost-benefit ratio at the standard length in *Caryocorbula* and *Parvilucina*, via a least-squares regression, no significant correlations were found. This lack of correlation suggests that changes in thickness, internal volume, and cost-benefit ratio at the standard length had no effect on predation intensity. This result is surprising in that Kelley (1989) found a negative correlation between thickness and drilling frequency. In this study samples with greater thickness at the standard length were drilled as often as samples with less thickness at the standard length. Drilling frequency in *Caryocorbula* was typically high in the Miocene (0.25-0.35), with the exception of the Boston Cliffs Member of the Choptank Formation (~0.05) (Fig. 7). Pliocene and Pleistocene drilling frequencies were typically low (0.00-0.08). *Parvilucina* drilling frequencies were highly variable and display no directional trend (Fig. 7). Temporal trends of drilling frequency in *Caryocorbula* and *Parvilucina* do not seem to match the cyclic rise and fall found by Kelley and Hansen (2003) for molluscan assemblages.

Did the Evolution of Anti-Predatory Morphology Affect Prey Effectiveness?

Prey effectiveness was compared to thickness, internal volume, and cost-benefit ratio at the standard length in *Caryocorbula* and *Parvilucina* using a least-squares regression. No significant correlations were found in either bivalve genus. The temporal trend of prey effectiveness in *Caryocorbula* displayed an increase from the Plum Point Marl Member to the Chowan River Formation. Prey effectiveness decreased dramatically in the Waccamaw Formation following the Plio-Pleistocene regional extinction (Stanley, 1986; Petuch, 1995). Low prey effectiveness values for *Caryocorbula* in the Waccamaw Formation are perplexing when one considers that cost-benefit ratio values were at their highest at this time, though this may be attributable to small sample size (n=14). Prey effectiveness in *Parvilucina* is characterized by consistently low values. *Caryocorbula* seemed to become better adapted to drilling predators than *Parvilucina*, as indicated by temporal change in prey effectiveness. The lack of correlation between the evolution of anti-predatory characters and prey effectiveness (despite the increase in the expression of anti-predatory morphology) in either genus suggests that the naticid predators outpaced the corbulid and lucinid prey evolutionarily. Kelley and Hansen (1993; 2003) reported that prey effectiveness in bivalve and gastropod faunas increased significantly from the Cretaceous to the Oligocene. This significant increase in prey effectiveness indicated that the evolution of prey defenses outpaced the evolution of the predator's ability to overcome these defenses. Conversely, Kelley and Hansen (2003; and contained references) reported no significant trend in prey effectiveness during the Neogene and Pleistocene. The lack of trends in prey effectiveness found in the Neogene and Pleistocene was interpreted as evolution of

the predator's ability to overcome prey defenses outpacing the evolution of prey defenses. The results of this study are consistent with the findings of Kelley and Hansen (2003).

Alternative Modes of Defense and Controls of Shell Morphology; or Complicating Factors when Tracing the Evolution of Morphology.

Unsuccessful predation must occur for prey to adapt to the hazard of the predator (Vermeij, 1982). If all attacks by the predator are successful, prey that possess more anti-predatory adaptations will not survive to pass on their characters unless the predator avoids them. Vermeij (1983) suggested that gastropods and bivalves have taken different evolutionary paths to deal with shell-breaking predation. He asserted that shell-breakage is nearly always lethal in bivalves due to the exposure of soft parts and leakage of chemical cues attracting predators. Shell-breakage is not as detrimental to gastropods. Gastropods have evolved specialized armor (i.e. high spires, narrow apertures, thick lips, etc.) to fend off predators in the subjugation phase of predation. Bivalves, however, have concentrated their evolutionary efforts in the recognition phase of predation. It seems to be more effective for bivalves to avoid the predator than to defend against it when it attacks. A potential manner to accomplish this would be for the bivalve to burrow deeper into the sediment, but is this traceable in the fossil record? Depth of burial may be reflected through pallial sinus length, which is highly correlated with siphon length (Stanley, 1970). One could trace the evolution of depth of burial, using the methodology applied in this study, and might predict that depth of burial would increase with time. *Caryocorbula* and *Parvilucina* do not have pallial sinuses; otherwise this possibility would have been investigated. It should be noted that many lucinids are deep burrowers,

despite the lack of a pallial sinus, and maintain communication above the sediment/water interface with a mucous-lined sandy tube substituting for an absent inhalant siphon and a very long exhalant siphon (Kelley, pers. comm.; Abbott, 1996; Lebata, 2001).

Bivalves may also utilize active escape defenses to avoid predators. Bivalves, such as *Donax variabilis*, burrow rapidly in the sediment (Stanley, 1970; personal observation). *Dinocardium robustum* (family: Cardiidae) uses its large foot to leap away from predators (G. Dietl, pers. comm.; Abbott, 1996). Some species of pectinids swim away from a disturbance by the rapid contracting and relaxing of the adductor muscle, "clapping" the valves (Stanley, 1970). All pectinids have eyes that allow them to detect changes in light and tentacles that can detect chemical cues and changes in water pressure (Abbott, 1996). It seems doubtful that the lucinids or corbulids considered in this study utilized active escape defenses. Studies addressing the ecology of these extant genera are seemingly absent from the literature however, inferences about their behavior can be made from what is known about their life mode and shell morphology. *Caryocorbula* does not have the shell morphology of a rapid burrower (blade- or disk-shaped valves) (Stanley, 1970). As previously mentioned, many lucinids are deep burrowers and maintain communication with the sediment/water interface by the construction of a mucous-lined sandy tube that is likely difficult to maintain if the bivalve were very active.

Certain life histories may confer an advantage to bivalves when dealing with predators. Bivalves may display rapid growth to reach a size refuge from predation (as there is an upper limit to the size of prey that naticids can handle). This strategy delays first reproduction, but may afford the organism more opportunities to reproduce in the

long run once in the size refuge. Conversely, a bivalve may remain small, but reach first reproduction at an earlier age. The organism would remain in danger of being eaten, but may reproduce before this occurs. Such possibilities may be examined by analyzing stable isotope data ($\delta^{18}O$ and $\delta^{13}C$) taken from bivalve specimens along an ontogenetic profile. Such profiles often reveal annual cycles of growth that can give insight into growth rates and age at first reproduction (Jones, 1998; Dietl et al., 2002).

Climate change may produce changes in shell morphology. Calcium carbonate is thermodynamically "cheaper" to deposit in warm water than cold (Lowenstam and Weiner, 1989). Changes in climate may regulate the extent to which a bivalve can deposit aragonite. Bivalves may be thicker during warm climates and thinner during cool climates. A cooling trend began in the warm Plum Point Marl time, reaching the coolest point during Little Cove Point time. Warm-temperate to sub-tropical climate characterized Windmill Point time. Similar conditions prevailed during Cobham Bay Member time, which ended in cooling. Yorktown time was characterized by warm conditions, slight cooling occurred in Chowan River time, and sub-tropical conditions occurred during Waccamaw time (Ward, 1992; Ward and Blackwelder, 1987; Petuch, 1997) (Table 1). Thickness trends of *Caryocorbula* and *Parvilucina* do not match trends predicted if morphology was strictly controlled by climate (Table 1).

Changes in primary productivity may also produce morphological changes in bivalves. An increase in productivity would result in an increased food supply for filter-feeding bivalves. One might predict that an increase in productivity would result in more robust shells. Teusch et al. (2002) found this to be the case in their investigation of Pleistocene to Recent turritellid gastropods in Chile. They found that significant

temporal and spatial variation in size and whorl height correlate with differences in productivity. Turritellids were larger and more robust during times of high productivity. One might expect similar results in the bivalves used in this study, as they and turritellids are both suspension-feeders. However, change in productivity may have less effect on lucinids than corbulids. Lucinids contain chemosymbiotic algae in their gills that produce glucose that is used by the clam as a significant portion of its nutrition (Cobabe, 1991; Lebata, 2001).

Ward and Blackwelder (1976) interpreted periods of high productivity in the Calvert and Choptank Formations as indicated by diatomaceous sediments. High productivity has been noted during this time from other regions in the world (R. Laws, pers. comm.). Ward and Blackwelder (1976) do not mention periods of high productivity in their description of lithologic units from the St. Mary's Formation through the Yorktown Formation. The Pliocene/Pleistocene mass extinction is interpreted as being caused by a reduction in primary productivity triggered by the formation of the Panamanian isthmus (Allmon, 2001). The decrease in thickness at the standard length in *Caryocorbula inaequalis* may be related to the reduction in productivity after the Choptank Formation was deposited. Changes in productivity do not seem to have an effect on the morphology of the other species.

Water energy may also have an effect on shell morphology. Gastropods on rocky shorelines are one example. Individuals that live in rocky intertidal environments are exposed to high-energy water, and are often more heavily armored than their counterparts living further offshore in less harsh environments (Vermeij, 1993). This factor may have had some effect on low thickness in *Parvilucina* from the Little Cove Point Member.

The Little Cove Point Member is interpreted as a quiet bay environment. The environment of deposition of the other intervals used in this study were interpreted as open marine shelf environments and were likely subject to similar water energies. Kelley (1989) found a decrease in thickness at the standard length relative to thicknesses found in previous stratigraphic intervals in the bivalve *Anadara* in the Little Cove Point Member, but these values are not dissimilar to thickness values in the Windmill Point Member indicating little influence from water energy on morphology. Water energy does not appear to have any major effect on morphology in either genus in any other environment examined.

Inducible defenses are another source of variation in shell morphology. Inducible defenses are defensive responses by the prey that are usually triggered by a chemical cue from the predator. They are often used when encounter rates between predator and prey are frequent but unpredictable (Harvell, 1990). Inducible defenses may only be used sporadically because of the costs incurred to the prey. Smith and Jennings (2000) found that *Mytilus edulis* juveniles grown in separate treatments containing the effluent of feeding drilling predators (*Nucella lapillus*) and feeding crushing predators (*Carcinus maenas*) were significantly thicker than *M. edulis* grown in the control with no predator effluent. Mussels grown in the effluent of the drilling gastropod were significantly thicker than mussels grown in the effluent of the crab. Smith and Jennings (2000) suggested that this increase in thickness occurred at the cost of linear growth, possibly delaying the mussel from reaching a size refuge from predation. Similar induced defenses have been found in the gastropod prey of crab predators (Trussell and Nicklin, 2002). Inducible defenses appear to be used sporadically in ecologic time, so how would

they be expressed in the fossil record? The fossil record rarely provides the resolution needed to detect such short term change, possibly with the exception of lagerstätten. Taxa that utilize inducible defenses may be indicated by a greater degree of variation in a given character at a specific time. In this study, for instance, when plotting thickness vs. length for a given taxon from a given stratigraphic interval, inducible defenses may be indicated by increased variation in thickness from the regression line. However, it would be difficult to distinguish the results of inducible defenses from "regular" natural geographic variation among populations.

Selection from multiple predators may also contribute to the evolution of bivalve morphology. Drilling naticids are not the sole predators of infaunal bivalves. Crabs are important predators of bivalve mollusks. Crabs possess a diverse array of shell-opening techniques that may or may not leave traces in the fossil record (Lau, 1987; Seed and Hughes, 1995). Crushing predation by crabs may result in an evolutionary increase in thickness of bivalve shells. Many modern fish ingest bivalves. Analysis of *Lagodon rhomboides* (pin fish) gut contents revealed whole articulated bivalves of similar size to those used in this study (personal observation). Such predation by fish is likely significant, though would leave no trace in the fossil record. Gut content analysis of the loggerhead sea turtle *Caretta caretta* showed that mollusks are an important fraction of its catholic diet (Lutz and Musick, 1997; Bjorndal, 1995). Sea turtle predation on molluscs may not be as important today, but was likely significant in pre-Columbian times (Jackson, 1997). Predators such as turtles and fish, which crush or swallow prey whole, are limited by the gape of their jaws in the size of prey that they can handle. This type of predation may result in a size increase of prey. The actions of multiple predators

may produce selection for the same traits (such as naticids and crabs), but determining which predator played the larger role in driving the evolution of anti-predatory traits is problematic. Inferences may be made by examining predation frequencies of various predators in modern settings.

Determining the cause of evolution, even within a few characters of an organism, can be quite complicated, and many factors must be examined. The evolution of anti-predatory morphology was examined in this study. The expression of anti-predatory morphology increased in *Caryocorbula conradi* and *Parvilucina crenulata*, as predicted. Alternate modes of defense and controls of shell morphology that could influence predicted patterns of anti-predatory morphology were evaluated and by and large discounted. The expression of anti-predatory morphology decreased in the time interval examined, contrary to prediction, in *Caryocorbula inaequalis*. This decrease in thickness and cost-benefit ratio may be related to the decline in productivity following the deposition of the Choptank Formation. The decrease in productivity did not seem to have any bearing on thickness, internal volume, nor cost-benefit ratio in *Parvilucina crenulata*, and was likely due to the dependence of lucinids upon chemosymbiotic bacteria for nutrition.

# CONCLUSIONS

- Three of nine hypotheses of change in anti-predatory morphology were confirmed.
- *Caryocorbula conradi* displayed significant increases in thickness and cost-benefit ratio, in accordance with the hypotheses.
- *Parvilucina crenulata* displayed a significant increase in cost-benefit ratio, in accordance with the hypotheses (though there were no significant changes in thickness nor internal volume when each character was considered individually).
- *Caryocorbula inaequalis* displayed a significant decrease in thickness and cost-benefit ratio, contrary to the hypotheses.
- Neither drilling frequency nor prey effectiveness was correlated with thickness, internal volume, or cost-benefit ratio at the standard length.
- *Caryocorbula* was better adapted to drilling predators than *Parvilucina*, but their naticid predators may have outpaced both evolutionarily.
- Decreasing primary productivity following the deposition of the Choptank Formation likely contributed to the decrease in thickness and cost-benefit ratio in *Caryocorbula inaequalis*.
- Other alternate modes of defense and controls of shell morphology that could affect predicted trends were considered, and were by and large discounted.

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# APPENDICES

## Appendix A. Locality Register

Calvert Formation:
Between Willows Beach and Camp Roosevelt, 2.8 km east of the intersection of Highway 2/4 and Pond Woods Rd., western shore of the Chesapeake Bay, Calvert Co., MD, North Beach 7.5 min. quadrangle.

Choptank Formation:
Boston Cliffs, Choptank River, just south of the Highway 331 bridge, Talbot Co., MD, Fowling Creek 7.5 min. quadrangle.

St. Marys Formation, Little Cove Point Member:
1.0 km south of Little Cove Point, western shore of the Chesapeake Bay, Calvert Co., MD, Solomons Island 7.5 min. quadrangle.
Langley's Bluff (of old literature), 7.3 km south of Cedar Point, 1.0 km below the mouth of Beaver Dam Creek, western shore of the Chesapeake Bay, St. Mary's Co., MD, St. Mary's City 7.5 min. quadrangle.
Deep Point, across St. Mary's River from St. Mary's City, MD, St. Mary's City 7.5 min. quadrangle.

St. Marys Formation, Windmill Point Member:
0.4 km below Chancellor's Point, left bank of the St. Mary's River, St. Mary's Co., MD, St. Mary's City 7.5 min. quadrangle.
Deep Point, across St. Mary's River from St. Mary's City, MD, St. Mary's City 7.5 min. quadrangle.

Eastover Formation, Cobham Bay Member:
Right bank of Urbanna Creek, 0.5 km above the Rte. 227 Bridge, Middlesex Co., VA, Urbanna 7.5 min. quadrangle.
0.8 km below Cobham Wharf, right bank of the Surrey River, Surrey Co., VA, Surrey 7.5 min. quadrangle.
Whiting Creek, Mouth of Whiting Creek on Rappahannock River, Saluda, VA, Saluda 7.5 min. quadrangle.
0.8 km above Mount Pleasant, right bank of the James River, Surrey Co., VA, Surrey 7.5 min. quadrangle.
Claremont and Sunken Meadow type section, 1.3 km below mouth of Sunken Meadow Creek on James River, Claremont, VA, Claremont 7.5 min. quadrangle.

Yorktown Formation, Rushmere Member:
Day's Point, 0.3 km southeast of Morgart's Beach, Isle of Wight Co., VA, Mulberry Island 7.5 min. quadrangle.
One mile downstream Tar River from Old Sparta, Tarboro 15 min. quadrangle.
Rushmere Wharf, west bank of the James River, Isle of Wight Co., VA, Bacon's Castle 7.5 min. quadrangle.

Yorktown Formation, Morgart's Beach Member:
Fort Boykins State Park, river bluffs on the south bank of the James River, Isle of Wight Co., VA, Mulberry Island 7.5 min. quadrangle.

Yorktown Formation, Moore House Member:
Fort Boykins State Park, river bluffs on the south bank of the James River, Isle of Wight Co., VA, Mulberry Island 7.5 min. quadrangle.
Chuckatuck Pit, Intersection of Rte. 10 and Rte. 32, Isle of Wight Co., VA, Benns Church 7.5 min. quadrangle.

Chowan River Formation:
Edenhouse Landing, 0.8 km above Edenhouse Point, right bank of the Chowan River, Bertie Co., NC, Edenton 15 min. quadrangle.
Bluff on the high bank of the Chowan River, 1.5 km upriver from Mount Gould Landing, Bertie Co., NC, Colerain 7.5 min. quadrangle.
Bluff on the right bank of the Chowan River, 0.4 miles downstream from Colerain Landing, Bertie Co., NC, Colerain 7.5 min. quadrangle.
Gomez Pit, Williams Corporation of Virginia, west side of Centerville Rd., about 0.5 km northwest of the intersection of Centerville and Kempsville Roads, Virginia Beach, VA, Kempsville 7.5 min. quadrangle.
1.8 km southeast of Hamilton, Roanoke River, Martin Co., NC, Hamilton 7.5 min. quadrangle.

Waccamaw Formation:
Old Dock, 300 ft. north of Highway 130, 0.6 miles northwest of intersection Highway 130 and State Road 1001, Columbus Co., NC, Old Dock 7.5 min. quadrangle.

## Appendix B. Data

Calvert Formation Plum Point Marl Member

*Caryocorbula inaequalis*

| L | thickness | msand |
|---|---|---|
| 6.79 | 0.53 | 0.03 |
| 7.04 | 0.43 | 0.034 |
| 7.38 | 0.62 | 0.038 |
| 6.86 | 0.76 | 0.037 |
| 7.2 | 0.61 | 0.034 |
| 8.09 | 0.79 | 0.042 |
| 7.5 | 0.72 | 0.031 |
| 7.71 | 0.79 | 0.037 |
| 7.61 | 0.64 | 0.045 |

*Parvilucina crenulata*

| L | thickness | msand |
|---|---|---|
| 3.93 | 0.2 | 0.009 |
| 3.94 | 0.23 | 0.01 |
| 4.45 | 0.23 | 0.012 |
| 3.61 | 0.18 | 0.007 |
| 4.71 | 0.26 | 0.015 |
| 5.05 | 0.31 | 0.023 |
| 5.03 | 0.22 | 0.02 |
| 4.8 | 0.24 | 0.013 |
| 3.71 | 0.25 | 0.009 |
| 4.94 | 0.28 | 0.015 |
| 4.26 | 0.21 | 0.009 |
| 4.89 | 0.23 | 0.02 |

*Parvilucina prunus*

| L | thickness | msand |
|---|---|---|
| 3.38 | 0.19 | 0.005 |
| 4.67 | 0.38 | 0.015 |
| 5.44 | 0.46 | 0.029 |
| 5.18 | 0.47 | 0.026 |
| 5.02 | 0.43 | 0.02 |
| 5.23 | 0.47 | 0.022 |
| 5.31 | 0.35 | 0.022 |
| 5.87 | 0.52 | 0.036 |
| 5.71 | 0.45 | 0.03 |
| 5.85 | 0.33 | 0.027 |
| 7.62 | 0.64 | 0.066 |
| 6.27 | 0.43 | 0.038 |
| 6.56 | 0.58 | 0.046 |
| 6.88 | 0.67 | 0.05 |
| 7.65 | 0.63 | 0.062 |
| 5.66 | 0.66 | 0.029 |
| 5.58 | 0.41 | 0.028 |
| 5.69 | 0.45 | 0.03 |
| 4.99 | 0.45 | 0.016 |
| 4.9 | 0.31 | 0.014 |
| 6.26 | 0.48 | 0.042 |
| 6.02 | 0.39 | 0.031 |
| 5.4 | 0.39 | 0.022 |
| 5.01 | 0.46 | 0.022 |
| 5.53 | 0.44 | 0.025 |
| 5.39 | 0.22 | 0.016 |
| 6.44 | 0.56 | 0.039 |
| 5.2 | 0.42 | 0.022 |
| 4.22 | 0.29 | 0.011 |

| | | |
|---|---|---|
| 5.45 | 0.51 | 0.028 |

Choptank Formation Boston Cliffs Member zone 19

*Caryocorbula inaequalis*

| L | thickness | msand |
|---|---|---|
| 6.16 | 0.38 | 0.017 |
| 4.7 | 0.27 | 0.007 |
| 4.78 | 0.37 | 0.006 |
| 5.09 | 0.32 | 0.008 |
| 5.46 | 0.3 | 0.014 |
| 6.45 | 0.4 | 0.019 |
| 6.54 | 0.47 | 0.021 |
| 6.58 | 0.43 | 0.019 |
| 5.95 | 0.42 | 0.015 |

St. Mary's Formation Little Cove Point Member

| *Caryocorbula inaequalis* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 7.29 | 0.54 | 0.0373 | 5.45 | 0.27 | 0.027 |
| 6.26 | 0.63 | 0.0284 | 5.12 | 0.24 | 0.021 |
| 6.01 | 0.46 | 0.02 | 3.93 | 0.21 | 0.008 |
| 7.47 | 0.67 | 0.033 | 3.86 | 0.2 | 0.006 |
| 8.31 | 0.92 | 0.046 | 3.66 | 0.22 | 0.007 |
| 8.93 | 0.59 | 0.0503 | 3.89 | 0.25 | 0.007 |
| 8.03 | 0.49 | 0.0547 | 3.69 | 0.19 | 0.009 |
| 8.65 | 0.63 | 0.0488 | 2.98 | 0.14 | 0.001 |
| 8.31 | 0.86 | 0.0497 | 4.31 | 0.23 | 0.014 |
| 8.43 | 0.57 | 0.055 | 3.76 | 0.19 | 0.008 |
| 7.54 | 0.51 | 0.03 | 4.06 | 0.18 | 0.01 |
| 9.26 | 0.84 | 0.0653 | 3.28 | 0.16 | 0.005 |
| 8.82 | 0.95 | 0.0537 | 3.72 | 0.13 | 0.007 |
| 9.48 | 0.67 | 0.0725 | 3.25 | 0.15 | 0.003 |
| 7.38 | 0.67 | 0.0315 | 3.21 | 0.16 | 0.004 |
| 9.38 | 0.65 | 0.0716 | 3.78 | 0.24 | 0.006 |
| 9.73 | 0.65 | 0.085 | 3.5 | 0.14 | 0.008 |
| 6.92 | 0.39 | 0.024 | 3.57 | 0.15 | 0.006 |
| 7.14 | 0.4 | 0.031 | 3.05 | 0.16 | 0.004 |
| 7.03 | 0.66 | 0.031 | 3.69 | 0.19 | 0.007 |
| | | | 3.39 | 0.13 | 0.005 |
| | | | 3.96 | 0.25 | 0.007 |
| | | | 3.76 | 0.16 | 0.009 |
| | | | 3.35 | 0.21 | 0.005 |
| | | | 3.77 | 0.19 | 0.007 |
| | | | 3.31 | 0.19 | 0.005 |
| | | | 3.07 | 0.16 | 0.005 |
| | | | 2.76 | 0.16 | 0.002 |
| | | | 3.15 | 0.19 | 0.003 |
| | | | 3.65 | 0.16 | 0.007 |

| | | |
|---|---|---|
| 4.77 | 0.39 | 0.018 |
| 3.53 | 0.22 | 0.008 |
| 5.13 | 0.24 | 0.021 |
| 3.88 | 0.22 | 0.008 |
| 4.36 | 0.16 | 0.01 |
| 4.12 | 0.22 | 0.013 |
| 4.54 | 0.21 | 0.015 |
| 3.95 | 0.18 | 0.006 |

St. Mary's Formation Windmill Point Member

| *Caryocorbula inaequalis* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 6.58 | 0.43 | 0.0268 | 3.86 | 0.23 | 0.01 |
| 6.29 | 0.73 | 0.022 | 3.37 | 0.16 | 0.006 |
| 8.63 | 0.65 | 0.0481 | 2.58 | 0.18 | 0.002 |
| 8.89 | 0.71 | 0.0602 | 3.6 | 0.16 | 0.008 |
| 9.51 | 0.74 | 0.0803 | 4.11 | 0.2 | 0.009 |
| 8.79 | 0.5 | 0.0522 | 4.34 | 0.22 | 0.017 |
| 9.17 | 0.8 | 0.079 | | | |
| 7.2 | 0.55 | 0.0312 | | | |
| 7.28 | 0.31 | 0.0343 | | | |
| 8 | 0.38 | 0.0502 | | | |
| 8.26 | 0.45 | 0.0514 | | | |
| 7.95 | 0.53 | 0.0407 | | | |
| 8.84 | 0.5 | 0.0656 | | | |
| 7.9 | 0.64 | 0.03 | | | |
| 6.75 | 0.6 | 0.017 | | | |

Eastover Formation Cobham Bay Member

| *Caryocorbula conradi* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 9.48 | 0.54 | 0.066 | 4.11 | 0.25 | 0.015 |
| 7.9 | 0.4 | 0.031 | 5.17 | 0.3 | 0.02 |
| 8.97 | 0.48 | 0.054 | 4.1 | 0.24 | 0.014 |
| | | | 3.52 | 0.39 | 0.008 |
| | | | 3.78 | 0.33 | 0.009 |
| | | | 4.55 | 0.21 | 0.013 |
| | | | 4.03 | 0.27 | 0.009 |
| | | | 3.71 | 0.35 | 0.005 |
| | | | 3.81 | 0.32 | 0.005 |
| | | | 3.7 | 0.2 | 0.007 |
| | | | 4.1 | 0.3 | 0.01 |
| | | | 3.95 | 0.28 | 0.009 |
| | | | 2.99 | 0.14 | 0.003 |
| | | | 3.41 | 0.27 | 0.003 |
| | | | 4.33 | 0.23 | 0.012 |
| | | | 3.41 | 0.28 | 0.004 |
| | | | 3.27 | 0.21 | 0.006 |

| | | |
|---|---|---|
| 2.72 | 0.17 | 0.004 |
| 2.64 | 0.21 | 0.003 |
| 5.11 | 0.34 | 0.02 |
| 3.38 | 0.23 | 0.005 |
| 3.85 | 0.23 | 0.009 |
| 4.36 | 0.33 | 0.01 |
| 5.71 | 0.27 | 0.023 |
| 4.35 | 0.22 | 0.012 |

Yorktown Formation Rushmere Member

| *Caryocorbula inaequalis* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 13.51 | 1.32 | 0.1668 | 5.23 | 0.43 | 0.0198 |
| 10.98 | 1.07 | 0.1511 | 4.45 | 0.46 | 0.0122 |
| 10.46 | 1.19 | 0.1365 | 4.9 | 0.37 | 0.0196 |
| 8.89 | 0.74 | 0.0473 | 5.48 | 0.35 | 0.0217 |
| 10.71 | 1.36 | 0.1151 | 2.82 | 0.21 | 0.0034 |
| 11.01 | 0.8 | 0.1264 | 5.12 | 0.39 | 0.0173 |
| 9.41 | 0.86 | 0.0602 | 3.71 | 0.28 | 0.006 |
| 11.46 | 1.36 | 0.1312 | 4.09 | 0.32 | 0.0099 |
| 8.05 | 0.52 | 0.0395 | 3.72 | 0.31 | 0.0067 |
| 7.14 | 0.4 | 0.0298 | 5.09 | 0.45 | 0.0167 |
| 9.49 | 0.55 | 0.0734 | 5.01 | 0.32 | 0.0141 |
| 6.83 | 0.35 | 0.0242 | 2.09 | 0.21 | 0.0006 |
| 7.63 | 0.51 | 0.035 | 3.93 | 0.25 | 0.0111 |
| 7.65 | 0.58 | 0.04 | 5.29 | 0.36 | 0.021 |
| 12.11 | 1.01 | 0.12 | 5.36 | 0.43 | 0.024 |
| 8.13 | 0.54 | 0.0575 | 5.52 | 0.34 | 0.02 |
| 9.99 | 0.78 | 0.0722 | 4.2 | 0.32 | 0.01 |
| 9.36 | 0.56 | 0.0603 | 3.96 | 0.3 | 0.007 |
| 10.71 | 0.67 | 0.0839 | 5.61 | 0.41 | 0.022 |
| 7.68 | 0.57 | 0.0346 | 3.98 | 0.29 | 0.011 |
| 8.05 | 0.67 | 0.034 | 5.2 | 0.37 | 0.018 |
| 8.07 | 0.61 | 0.0359 | 4.65 | 0.4 | 0.014 |
| 8.62 | 0.56 | 0.0527 | 4.16 | 0.29 | 0.009 |
| 8.71 | 0.5 | 0.0702 | 4.07 | 0.32 | 0.006 |
| 9.48 | 0.7 | 0.0487 | 5.2 | 0.36 | 0.018 |
| 9.54 | 0.55 | 0.0625 | 3.89 | 0.3 | 0.005 |
| 10.4 | 0.59 | 0.0732 | 3.82 | 0.35 | 0.006 |
| 6.85 | 0.67 | 0.0256 | 3.46 | 0.28 | 0.004 |
| 4.97 | 0.4 | 0.0108 | 4.01 | 0.34 | 0.009 |
| 8.8 | 0.53 | 0.0421 | 3.88 | 0.31 | 0.008 |
| 10.83 | 0.54 | 0.1038 | 3.42 | 0.26 | 0.005 |
| 10.19 | 0.53 | 0.0774 | 3.46 | 0.27 | 0.005 |
| 10.23 | 0.83 | 0.0824 | 3.87 | 0.26 | 0.008 |
| 8.07 | 0.32 | 0.036 | 7.57 | 0.63 | 0.055 |
| 7.94 | 0.58 | 0.0403 | 9.11 | 0.78 | 0.077 |
| 10.58 | 0.74 | 0.0827 | 10.23 | 0.64 | 0.126 |

| | | | | | |
|---|---|---|---|---|---|
| 7.15 | 0.6 | 0.0224 | 7.74 | 0.66 | 0.062 |
| 11.92 | 1.38 | 0.1301 | 9.1 | 0.74 | 0.085 |
| 7.27 | 0.55 | 0.0247 | 8.14 | 0.59 | 0.058 |
| 14.06 | 1.31 | 0.215 | 8.11 | 0.65 | 0.072 |
| | | | 7.08 | 0.64 | 0.06 |
| | | | 7.82 | 0.47 | 0.063 |
| | | | 7.38 | 0.73 | 0.055 |
| | | | 7.46 | 0.49 | 0.05 |
| | | | 7.79 | 0.51 | 0.049 |
| | | | 7.8 | 0.54 | 0.047 |
| | | | 6.36 | 0.45 | 0.034 |
| | | | 5.6 | 0.53 | 0.023 |
| | | | 5.79 | 0.44 | 0.024 |
| | | | 4.73 | 0.28 | 0.014 |
| | | | 5.49 | 0.36 | 0.017 |
| | | | 5.65 | 0.47 | 0.021 |
| | | | 4.75 | 0.34 | 0.016 |
| | | | 4.95 | 0.25 | 0.017 |
| | | | 5.32 | 0.25 | 0.02 |
| | | | 4.11 | 0.38 | 0.009 |
| | | | 7.06 | 0.37 | 0.04 |
| | | | 4.36 | 0.3 | 0.013 |
| | | | 4.77 | 0.38 | 0.014 |
| | | | 4.8 | 0.4 | 0.014 |
| | | | 2.88 | 0.2 | 0.001 |
| | | | 4.91 | 0.37 | 0.015 |
| | | | 3.76 | 0.17 | 0.005 |
| | | | 3.17 | 0.19 | 0.001 |
| | | | 4.09 | 0.26 | 0.012 |
| | | | 4.77 | 0.33 | 0.016 |
| | | | 3.71 | 0.24 | 0.006 |

Yorktown Formation Morgart's Beach Member

| | *Parvilucina crenulata* | |
|---|---|---|
| L | thickness | msand |
| 6.24 | 0.38 | 0.032 |
| 5.23 | 0.39 | 0.018 |
| 5.36 | 0.39 | 0.023 |
| 6.3 | 0.35 | 0.033 |
| 5.07 | 0.32 | 0.017 |
| 4.4 | 0.36 | 0.014 |
| 4.42 | 0.31 | 0.014 |
| 5.71 | 0.38 | 0.033 |
| 4.64 | 0.36 | 0.015 |
| 6.07 | 0.34 | 0.03 |
| 3.81 | 0.17 | 0.009 |
| 5.31 | 0.32 | 0.025 |
| 4.5 | 0.33 | 0.017 |

| | | |
|---|---|---|
| 5.38 | 0.32 | 0.018 |
| 6.04 | 0.38 | 0.042 |
| 3.37 | 0.22 | 0.004 |
| 3.43 | 0.16 | 0.008 |
| 4.38 | 0.36 | 0.014 |
| 4.86 | 0.23 | 0.015 |
| 4.68 | 0.32 | 0.013 |

Yorktown Formation Moore House Member

| *Corbula (Caryocorbula) conradi* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 9.95 | 0.5 | 0.0816 | 6.77 | 0.5 | 0.039 |
| 8.41 | 0.62 | 0.0433 | 5.51 | 0.32 | 0.019 |
| 9.3 | 0.48 | 0.0631 | 4.74 | 0.26 | 0.009 |
| 9.1 | 0.46 | 0.0605 | 4.53 | 0.31 | 0.012 |
| 9.87 | 0.75 | 0.0621 | 4.12 | 0.3 | 0.009 |
| 9.63 | 0.64 | 0.0886 | 4.3 | 0.24 | 0.013 |
| 9.68 | 0.59 | 0.0703 | 4.08 | 0.29 | 0.007 |
| 7.01 | 0.32 | 0.023 | 3.88 | 0.29 | 0.006 |
| 7.48 | 0.66 | 0.0335 | 6.67 | 0.42 | 0.046 |
| 7.61 | 0.6 | 0.0332 | 5.47 | 0.35 | 0.02 |
| 7.13 | 0.43 | 0.0328 | 5.55 | 0.3 | 0.021 |
| 7.11 | 0.64 | 0.0306 | 6.46 | 0.39 | 0.033 |
| 8.05 | 0.45 | 0.0374 | 5.72 | 0.35 | 0.024 |
| 7.36 | 0.61 | 0.029 | 5.33 | 0.32 | 0.024 |
| 7.82 | 0.94 | 0.055 | 5.48 | 0.32 | 0.019 |
| 8.02 | 0.92 | 0.047 | 4.8 | 0.42 | 0.018 |
| 6.94 | 0.77 | 0.03 | 5.32 | 0.36 | 0.02 |
| 7.07 | 0.69 | 0.033 | 4.6 | 0.37 | 0.012 |
| 7.21 | 0.53 | 0.022 | 4.04 | 0.29 | 0.008 |
| 8.2 | 0.74 | 0.048 | 4.71 | 0.34 | 0.013 |
| 6.55 | 0.59 | 0.02 | 4.18 | 0.25 | 0.007 |
| 6.91 | 0.51 | 0.023 | 4.22 | 0.34 | 0.011 |
| 7.66 | 0.69 | 0.033 | 4.13 | 0.34 | 0.004 |

| *Corbula (Caryocorbula) inaequalis* | | | | | |
|---|---|---|---|---|---|
| L | thickness | msand | 4.49 | 0.31 | 0.012 |
| 8.68 | 0.97 | 0.0634 | 4.68 | 0.3 | 0.011 |
| 10.77 | 0.82 | 0.1218 | 4.19 | 0.29 | 0.009 |
| 7.13 | 0.46 | 0.0376 | 3.89 | 0.16 | 0.007 |
| 8.36 | 0.63 | 0.0327 | 3.46 | 0.26 | 0.005 |
| 8.65 | 0.81 | 0.0588 | 3.67 | 0.31 | 0.007 |
| 7.6 | 0.75 | 0.0388 | 4.09 | 0.27 | 0.006 |
| 7.46 | 0.52 | 0.0335 | 3.48 | 0.27 | 0.005 |
| 8.51 | 1.02 | 0.043 | 3.65 | 0.33 | 0.004 |
| 5.3 | 0.29 | 0.0147 | 3.41 | 0.26 | 0.002 |
| 7.38 | 0.38 | 0.0343 | 5.37 | 0.37 | 0.021 |
| 7.62 | 0.63 | 0.0351 | 5.26 | 0.29 | 0.024 |
| 7.45 | 0.4 | 0.0317 | 4.44 | 0.33 | 0.014 |
| | | | 4.15 | 0.32 | 0.007 |

| | | |
|---|---|---|
| 3.93 | 0.3 | 0.009 |
| 3.74 | 0.32 | 0.005 |
| 3.91 | 0.32 | 0.01 |
| 4.06 | 0.3 | 0.008 |
| 4.38 | 0.33 | 0.009 |
| 3.41 | 0.26 | 0.002 |

Chowan River Formation

| *Caryocorbula conradi* | | | *Parvilucina crenulata* | | |
|---|---|---|---|---|---|
| L | thickness | msand | L | thickness | msand |
| 8.23 | 0.46 | 0.049 | 7.23 | 0.37 | 0.043 |
| 13.79 | 0.82 | 0.2072 | 8.08 | 0.55 | 0.057 |
| 12.49 | 0.45 | 0.1601 | 5.6 | 0.41 | 0.021 |
| 9.41 | 0.7 | 0.089 | 5.3 | 0.32 | 0.019 |
| 10.02 | 0.99 | 0.0664 | 5.43 | 0.35 | 0.018 |
| 8.48 | 0.6 | 0.0546 | 8.42 | 0.43 | 0.07 |
| 9.67 | 0.74 | 0.0881 | 7.35 | 0.4 | 0.05 |
| 6.31 | 0.57 | 0.019 | 5.49 | 0.38 | 0.016 |
| 8.74 | 0.93 | 0.0562 | 4.45 | 0.33 | 0.005 |
| 8.11 | 0.64 | 0.0368 | 7.93 | 0.49 | 0.064 |
| 8.47 | 0.73 | 0.05 | 5.39 | 0.37 | 0.022 |
| 7.16 | 0.82 | 0.0325 | 3.94 | 0.3 | 0.009 |
| 13.94 | 1.5 | 0.155 | 8.63 | 0.66 | 0.078 |
| 14.13 | 0.78 | 0.17 | 7.59 | 0.59 | 0.052 |
| 10.59 | 0.95 | 0.096 | 5.47 | 0.43 | 0.026 |
| 8.56 | 0.66 | 0.058 | 4.35 | 0.36 | 0.008 |
| 7.26 | 0.62 | 0.029 | 6.65 | 0.51 | 0.033 |
| 7.11 | 0.61 | 0.026 | 8.8 | 0.59 | 0.078 |
| 7.15 | 0.88 | 0.023 | 8.32 | 0.44 | 0.067 |
| 5.8 | 0.69 | 0.014 | 5.89 | 0.41 | 0.026 |
| 6.56 | 0.68 | 0.023 | 6.76 | 0.34 | 0.034 |
| 11.42 | 0.59 | 0.094 | 6.75 | 0.39 | 0.034 |
| 8.27 | 1.02 | 0.035 | 6.68 | 0.51 | 0.031 |
| 7.2 | 0.45 | 0.023 | 5.65 | 0.36 | 0.016 |
| 7.45 | 0.64 | 0.027 | 4.16 | 0.25 | 0.009 |
| 4.81 | 0.49 | 0.005 | 8.8 | 0.59 | 0.078 |
| 4.78 | 0.42 | 0.002 | 8.32 | 0.44 | 0.067 |
| 5.65 | 0.57 | 0.01 | 5.89 | 0.41 | 0.026 |
| 6.45 | 0.58 | 0.015 | 6.76 | 0.34 | 0.034 |
| 6.97 | 0.79 | 0.019 | 6.75 | 0.39 | 0.034 |
| 7.95 | 0.92 | 0.041 | 6.68 | 0.51 | 0.031 |
| 6.67 | 0.77 | 0.02 | 5.65 | 0.36 | 0.016 |
| 5.56 | 0.57 | 0.013 | 4.16 | 0.25 | 0.009 |
| 6.51 | 0.64 | 0.017 | 6.75 | 0.45 | 0.038 |
| 12.63 | 1.24 | 0.141 | 6.84 | 0.47 | 0.042 |
| 6.05 | 0.62 | 0.015 | 5.68 | 0.35 | 0.025 |
| 6.89 | 0.79 | 0.022 | 6.47 | 0.39 | 0.035 |
| 5.09 | 0.44 | 0.009 | 6.03 | 0.39 | 0.031 |

| | | | | | |
|---|---|---|---|---|---|
| 5.56 | 0.58 | 0.012 | 5.96 | 0.41 | 0.031 |
| 5.15 | 0.33 | 0.009 | 6.57 | 0.39 | 0.045 |
| 6.87 | 0.55 | 0.021 | 4.51 | 0.24 | 0.013 |
| 5.56 | 0.52 | 0.012 | 5.97 | 0.32 | 0.028 |
| 6.71 | 0.69 | 0.033 | 4.38 | 0.25 | 0.01 |
| 6.93 | 0.85 | 0.025 | 4.53 | 0.25 | 0.009 |
| 6.68 | 0.55 | 0.025 | 4.14 | 0.28 | 0.006 |
| 7.3 | 0.79 | 0.026 | 4.04 | 0.24 | 0.007 |
| 7.73 | 0.65 | 0.028 | 4.52 | 0.29 | 0.009 |
| 7.6 | 0.76 | 0.028 | 3.86 | 0.26 | 0.005 |
| 8.36 | 0.82 | 0.041 | 4.89 | 0.21 | 0.008 |
| 9.07 | 0.69 | 0.074 | 4.65 | 0.24 | 0.011 |
| 5.2 | 0.54 | 0.015 | 6.22 | 0.3 | 0.03 |
| 6.12 | 0.56 | 0.018 | 4.53 | 0.26 | 0.014 |
| 9.05 | 0.86 | 0.061 | 2.75 | 0.18 | 0.002 |
| 7.04 | 0.55 | 0.034 | 5.61 | 0.41 | 0.02 |
| 7.68 | 0.62 | 0.025 | 3.74 | 0.31 | 0.008 |
| 11.77 | 0.62 | 0.098 | 4.04 | 0.3 | 0.008 |
| 7.77 | 0.34 | 0.041 | 3.98 | 0.29 | 0.009 |
| 9.16 | 0.38 | 0.048 | 3.94 | 0.25 | 0.008 |
| 9.5 | 0.45 | 0.065 | 3.4 | 0.18 | 0.006 |
| 11.25 | 0.74 | 0.078 | 5.45 | 0.35 | 0.021 |
| 11.23 | 0.71 | 0.102 | 4.78 | 0.38 | 0.015 |
| 11.65 | 0.5 | 0.095 | 3.47 | 0.22 | 0.005 |
| 13.44 | 0.97 | 0.112 | 3.83 | 0.2 | 0.008 |
| 13.6 | 1.24 | 0.165 | 3.18 | 0.14 | 0.004 |
| 14.07 | 1.07 | 0.223 | 3.4 | 0.26 | 0.005 |
| 14.68 | 1.16 | 0.242 | 3.36 | 0.3 | 0.006 |
| 10.49 | 1.08 | 0.0968 | 4.62 | 0.34 | 0.012 |
| 12.76 | 0.84 | 0.1393 | 4.61 | 0.36 | 0.012 |
| 9.61 | 0.83 | 0.0432 | 4.96 | 0.3 | 0.017 |
| 8.49 | 0.87 | 0.048 | 5.79 | 0.35 | 0.028 |
| 10.8 | 0.93 | 0.0842 | 6.38 | 0.48 | 0.032 |
| 11.26 | 0.87 | 0.1135 | 6.25 | 0.41 | 0.03 |
| 11.24 | 0.97 | 0.0876 | 6.27 | 0.48 | 0.034 |
| 9.41 | 0.78 | 0.0682 | 6.9 | 0.4 | 0.042 |
| 14.33 | 1.16 | 0.2179 | 8 | 0.53 | 0.065 |
| 12.35 | 0.85 | 0.1066 | 8.03 | 0.51 | 0.084 |
| 9.98 | 1.06 | 0.071 | 5.45 | 0.23 | 0.021 |
| 12.09 | 0.88 | 0.16 | 5.01 | 0.33 | 0.017 |
| 10.91 | 0.72 | 0.121 | 5.18 | 0.36 | 0.018 |
| | | | 4.53 | 0.32 | 0.012 |
| | | | 4.76 | 0.33 | 0.011 |
| | | | 4.68 | 0.38 | 0.013 |
| | | | 3.52 | 0.26 | 0.006 |
| | | | 3.17 | 0.26 | 0.004 |
| | | | 4.69 | 0.27 | 0.012 |
| | | | 4.6 | 0.32 | 0.012 |

| | | |
|---|---|---|
| 4.17 | 0.29 | 0.012 |
| 4.8 | 0.29 | 0.017 |
| 4.5 | 0.34 | 0.014 |
| 3.35 | 0.15 | 0.005 |
| 3.23 | 0.24 | 0.006 |

*Parvilucina multilineata*

| L | thickness | msand |
|---|---|---|
| 6.25 | 0.38 | 0.053 |
| 4.88 | 0.3 | 0.02 |
| 6.23 | 0.29 | 0.04 |
| 5.53 | 0.29 | 0.023 |
| 5.82 | 0.38 | 0.035 |
| 3.15 | 0.21 | 0.004 |
| 4.31 | 0.33 | 0.008 |
| 5.74 | 0.38 | 0.023 |
| 4.8 | 0.41 | 0.012 |
| 2.45 | 0.22 | 0.002 |
| 4.22 | 0.31 | 0.01 |
| 5.15 | 0.36 | 0.015 |
| 5.29 | 0.34 | 0.02 |
| 5.22 | 0.34 | 0.019 |
| 5.85 | 0.52 | 0.023 |
| 6.26 | 0.4 | 0.027 |

Waccamaw Formation

*Caryocorbula conradi*

| L | thickness | msand |
|---|---|---|
| 6.27 | 0.65 | 0.016 |
| 7.43 | 0.75 | 0.027 |
| 9.67 | 0.59 | 0.055 |
| 10.33 | 0.83 | 0.051 |
| 4.88 | 0.3 | 0.008 |
| 5.36 | 0.54 | 0.014 |
| 5.76 | 0.51 | 0.012 |
| 6.1 | 0.48 | 0.015 |
| 6.35 | 0.65 | 0.018 |
| 6.34 | 0.74 | 0.015 |
| 6.92 | 0.72 | 0.025 |
| 7.2 | 0.58 | 0.024 |
| 8.42 | 0.63 | 0.035 |
| 7.97 | 1.68 | 0.027 |

*Parvilucina multilineata*

| L | thickness | msand |
|---|---|---|
| 6.36 | 0.42 | 0.034 |
| 2.76 | 0.17 | 0.001 |
| 4.08 | 0.19 | 0.01 |
| 4.92 | 0.5 | 0.019 |
| 5.41 | 0.32 | 0.023 |
| 5.25 | 0.28 | 0.028 |
| 5.17 | 0.31 | 0.023 |
| 5.27 | 0.28 | 0.025 |
| 5.98 | 0.41 | 0.036 |

Appendix C. Recipe for Moon Snail Steaks

Meat should be removed raw. Slip a thin knife down the inside of the aperture, and cut across the opening. This will sever the columellar muscle, releasing animal.

Remove the soft spiral-shaped organs, slice off the operculum, and remove the head.

Slice meat into ½ inch steaks.

Sprinkle with meat tenderizer and pound with a meat hammer. Let meat sit in refrigerator overnight.

Dip steaks in egg wash and coat in flour and Creole seasoning. Fry until brown. Season with salt and pepper to taste.

# BIOGRAPHICAL SKETCH

John Warren Huntley was born in Fletcher, North Carolina, on August 11, 1977. After graduating from North Henderson High School in 1995, he attended Appalachian State University. While at ASU, John majored in geology, mapped geology in the Dolomites of the Italian Alps, and became affectionately known as the "rock nerd." Upon his graduation with a BS in 2000, John worked for a short period as transportation engineering geologist with the NC Department of Transportation. John began his graduate study in August of 2000 at the University of North Carolina at Wilmington, where his passion for the study of molluscs and evolution was developed under the mentorship of Dr. Patricia Kelley. John graduated from UNC Wilmington in 2003, and intends to begin doctoral study at Virginia Polytechnic Institute and State University.